121(3570)

Proceedings of the United States National Museum

SMITHSONIAN INSTITUTION • WASHINGTON, D.C.

Volume 121 1967 Number 3570

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SMITHSONIAN PRESS

Proceedings of
the United States
National Museum

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REVISION OF THE FAMILY PANDARIDAE (COPEPODA: CALIGOIDA)[1]

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In 1907, C. B. Wilson published a revision of the subfamily Pandarinae as part of a series of papers dealing with caligoid copepods. We now recognize that much of this work was superficial, containing descriptions of species often incomplete and inadequately figured; nevertheless, it served to focus attention on a group of parasites, caligoid copepods, which were then and are still today poorly known in most cases.

Between 1960 and 1965 I collected and solicited material of the family Pandaridae from as many different areas as possible. As a result of this accumulation of material and data, I feel that a revision of the family is in order. Ecological relationships are now more evident than before.

Because of inadequate species descriptions that exist for most members of this family, positive identification of material is often difficult. This results in the publication of records that obscure our understanding of existing host-parasite relationships. I believe that, in most cases, I have examined enough samples of members of this

[1] Modified from a Ph. D. dissertation submitted to Boston University, Boston, Mass.

group to be able to draw a clearer picture. Also, as a result of these collections, I have been able better to define important taxonomic characters and to discount others on which new species descriptions have often been based. It is with the foregoing in mind that I have made the following family revision. The Pandaridae as defined here is composed of 12 genera and 33 species.

The material examined was preserved in 10 percent formalin or 70 percent ethyl alcohol. For detailed examination of the appendages, the copepods were dissected in lactic acid and mounted in Hoyer's mounting medium. Whole specimens were often treated with 5 percent potassium hydroxide to render them more transparent. No distortion was noticed by this method.

All drawings were made with the aid of a camera lucida. The letter following the explanation of the figure refers to the scale at which it was drawn. In all text tabulations, Roman numerals refer to spines, Arabic numerals to setae.

All specimens are deposited in the U.S. National Museum unless otherwise designated.

I wish to acknowledge the constant encouragement and helpful advice offered by Dr. Arthur Humes, Boston University, during the course of this study.

I also wish to acknowledge the following persons who generously donated or loaned to me material for study: Dr. Thomas E. Bowman and Dr. Robert Gibbs, U.S. National Museum; Dr. Eugenie Clark, Cape Haze Marine Laboratory, Fla.; Dr. Richard Gooding, University of Singapore; Mr. Ju Shey Ho, Boston University; Miss Leonie Joubert, Oceanographic Research Institute, South Africa; Mr. Susumu Kato, California Fish and Wildlife Service; and Dr. Jan Stock, Zoological Museum, Amsterdam.

A portion of this work was supported by the National Science Foundation as a part of the U.S. Program in Biology, International Indian Ocean Expedition.

Family Pandaridae Milne-Edwards, 1840

FEMALE.—Body caligiform, usually with dorsal plates. First thoracic segment fused with cephalon. Thoracic segments 2–4 free. Genital segment conspicuous. Abdomen of 1 or 2 segments with or without dorsal plates. Oral area with or without adhesion pads. First antenna 2-segmented. Mandible in form of stylet with 10–12 apical teeth. Mandible inserted within mouth tube. Maxilliped with terminal claw. Legs 1–4 biramose. Leg 5 reduced. Egg strings consisting of long strings of eggs arranged in linear series.

MALE.—Body caligiform, without dorsal plates. First thoracic

segment fused with cephalon. Thoracic segments 2–4 free. Oral area generally as in female. Legs 1–4 biramose, rami always with long plumose setae. Legs 5 and 6 present. Abdomen 1- or 2-segmented. Caudal rami large.

Discussion.—Members of the family Pandaridae are generally considered to be parasites of elasmobranch fishes. Occasionally investigators report these copepods from teleost fish, but occurrence on such hosts is undoubtedly accidental and does not indicate the true host. The copepods are found on the body surface, cloacal aperture, gills and gill arches, mouth, and nasal passages. Those which are found on the body surface are often heavily pigmented; those in more protected areas are devoid of pigment.

These parasites are well adapted for attachment to the host, the female more so than the male. The principal attachment structure is the maxilliped. In the case of *Perissopus* the maxilliped becomes cemented to the host. Adhesion pads scattered over the ventral surface of the parasite seem to help resist its sliding over the surface of the host. The pads do not actually attach to the host but rather have surface striations for increased friction.

Locomotion is usually restricted to the males. The swimming legs of the females are often lamelliform (bearing reduced setae) and probably afford increased area for respiration with a reduction in the swimming function. Males are not so modified and undoubtedly move much more freely than the female.

The life history of pandarid copepods is still unknown. Wilson (1907) has outlined a composite life history of this group based on fragments of information from various representative caligoids. In general, the life history includes the following stages: egg, nauplius, copepodid, chalimus, and adult. The number of molts between stages is completely unknown for this group. The nauplius is of the usual copepod form with 3 pairs of anterior appendages. This stage is apparently free in the plankton and undoubtedly of short duration. The copepod attaches to the host as a copepodid (="metanauplius," Wilson 1907). The second antenna of this stage is greatly enlarged and projects anteriorly. The body of the copepodid is divided into a cephalon, 2 thoracic segments, and a fused genital segment-abdomen with rami attached distally. It is not clear whether this stage lasts for more than 1 molt. The chalimus assumes a body form similar to the adult. Wilson (1907) describes the chalimus stage as seen in *Perissopus dentatus*. The chalimus stage of caligoid copepods is characterized by the presence of a frontal filament. This is produced by glands in the anterior portion of the cephalon and serves to attach the copepod to the host. Wilson's description includes this structure. I have collected occasional chalimus stages in the genera *Pandarus*

and *Echthrogaleus* and have not observed this filament. More material will eventually show the true nature of this structure in pandarid copepods. The chalimus apparently undergoes a series of molts, increasing the segmentation until the adult form is reached. Lewis (1963) has described the life history stages of *Lepeoptheirus dissimulatus* Wilson. This copepod includes the following stages in its life history: nauplius (first and second), copepodid (1 stage), chalimus (6 stages), and adult. The life history of pandarids is probably quite similar. Heegaard (1947) described 2 copepodid stages for *Caligus curtus* (Muller).

The family Pandaridae is composed of 2 well-defined groups on the basis of external characters of both sexes. These characters are included in the key below. Group I includes the following genera: *Pandarus*, *Pseudopandarus*, *Phyllothyreus*, *Gangliopus*, *Perissopus*, and *Pannosus*. Group II includes: *Dinemoura*, *Demoleus*, *Pagina*, *Echthrogaleus*, *Nesippus*, and *Paranesippus*. Keys to the genera of females of the 2 groups also are provided below (not enough information is available to construct a key to the males).

Key to Groups and Genera of Pandaridae

FEMALES

Dorsal thoracic plates present on segments 2–4; penultimate segment of second maxilla with 2 prominent distal spines . . . . . GROUP I

Dorsal thoracic plates, if present, on segment 4 only; penultimate segment of second maxilla with 1 spine and a patch of spinules or setules . GROUP II

MALES

Outer distal corner of last endopod segment of leg 3 smooth . . . . GROUP I

Outer distal corner of last endopod segment of leg 3 modified with roughened areas and short spines . . . . . GROUP II

GENERA OF GROUP I FEMALES

1. Dorsal thoracic plates of segment 3 extending beyond plates of segment 3 . 3
   Dorsal thoracic plates of segment 3 not extending beyond plates of segment 2 2
2. Abdomen and caudal rami hidden dorsally . . . . . **Perissopus**
   Abdomen and caudal rami visible dorsally . . . . . **Pandarus**
3. Plates of segment 2 large, overlapping those of segment 3 4
   Plates of segment 2 reduced and lateral to those of segment 3 5
4. Maxilliped with spatulate tip . . . . . **Pannosus**
   Maxilliped with pointed tip . . . . . **Phyllothyreus**
5. Maxilliped with pointed tip, genital segment less than ½ body length. **Gangliopus**
   Maxilliped with spatulate tip, genital segment at least ½ body length. **Pseudopandarus**

GENERA OF GROUP II FEMALES

1. Abdomen 2-segmented 2
   Abdomen 1-segmented 3
2. Fourth leg lamelliform . . . . . **Dinemoura**
   Fourth leg not lamelliform . . . . . **Pagina**
3. Fourth leg lamelliform . . . . . **Echthrogaleus**
   Fourth leg not lamelliform 4
4. Abdomen with large dorsal plate . . . . . **Demoleus**
   Abdomen without dorsal plate 5
5. Exopods of legs 1–3 3-segmented . . . . . **Paranesippus**
   Exopods of legs 1–3 2-segmented . . . . . **Nesippus**

Genus *Pandarus* Leach, 1816

Pandarus Leach, 1816, p. 405. [Type-species: *P. bicolor.*]
Caligus.—Lamarck, 1818, p. 137. [Refers to *C. bicolor* only.]
Nogagus Leach, 1819, p. 536.

FEMALE.—Frontal plate distinctly separate. First thoracic segment fused with cephalon. Thoracic segments 2–4 free, bearing dorsal plates. Dorsal plates of segment 3 never extending beyond plate of segment 2. Plates of segment 4 fused basally. Abdomen 1-segmented with dorsal plate. Abdomen (or its plate) visible dorsally and attached to distal end of genital segment. Caudal rami lateral to abdomen. First antenna 2-segmented. Adhesion pads present on cephalon in association with first and second antennae and maxilliped; pads also located on ventral surface of posterior corners of cephalon. Claw of maxilliped spatulate. Legs 1–4 biramose, rami of legs 1–3 2-segmented. Rami of leg 4 1-segmented. Leg 5 present. Egg strings long and straight.

MALE.—No dorsal plates present. Cephalic appendages in general like those of female. Legs 1–4 biramose, all rami 2-segmented and bearing plumose setae. Fifth and sixth legs present. Leg 3 endopod unmodified.

DISCUSSION.—Since 1816, 29 species have been described and assigned to this genus. Only 10 of these remain valid today. The synonymies are discussed with the species descriptions. I propose to designate each of the following 4 species described by Hesse in 1883 as a nomen dubium on the basis that the descriptions and figures are so poor that it is impossible to assign these to any known taxon: *Pandarus mustelilaevis*, *Pandarus unicolor*, *Pandarus spinaciiachantias*, and *Pandarus carchiiglaucus*.

Members of the genus *Pandarus* are parasites on the body surface of the host. They have been reported from both pelagic and inshore species and are the most frequently encountered pandarid copepod. The females of some species are heavily pigmented and those of others

show some signs of pigmentation. They frequently occur in clusters of more than 100 individuals on the fins of the shark.

Members of this genus can easily be separated from other genera on the basis of the arrangement of the dorsal thoracic plates and the nature of the caudal rami.

Key to Adult Females of *Pandarus*

1. Dorsal plate of thoracic segment 2 extending only as far as the posterior edge of the plate of segment 3 . . . . . BICOLOR GROUP. 2
   Dorsal plate of thoracic segment 2 extending well beyond posterior edge of plate of segment 3 . . . . . CRANCHII GROUP. 4
2. Cephalon only ⅓ of total body length; caudal rami small, scarcely visible dorsally . . . . . **bicolor**
   Cephalon about ½ of total body length; caudal rami easily visible dorsally . 3
3. Caudal rami long, about 3 times as long as dorsal abdominal plate and extending well beyond it; posterior edge of plate of segment 4 without conspicuous sinus . . . . . **niger**
   Caudal rami only about 1½ times as long as dorsal abdominal plate and extending only slightly beyond it; posterior edge of plate of segment 4 with deep sinus . . . . . **carcharhini**
4. Caudal rami with the inner basal half expanded to broad lobe . . **smithii**
   Caudal rami without such a lobe 5
5. Caudal rami not extending more than ⅔ length of dorsal abdominal plate. **satyrus**
   Caudal rami extending at least to tip of dorsal abdominal plate or well beyond it 6
6. Dorsal plates of thoracic segments 3 and 4 fused and with broad posterior sinus 7
   Dorsal plates of thoracic segments 3 and 4 divided by deep sinus into 2 nearly separate lobes 9
7. Dorsal abdominal plate subtriangular; eye spots separated in fully pigmented forms . . . . . **cranchii**
   Dorsal abdominal plate subcircular; body may or may not be darkly pigmented 8
8. Most of body darkly pigmented but eye spots connected by median posterior line . . . . . **sinuatus**
   Body only slightly pigmented with pigment usually confined to anterior portion of cephalon and plate of fourth thoracic segment . . . **floridanus**
9. Thoracic plate of segment 2 extending to posterior tip of thoracic plate of segment 4 . . . . . **zygaenae**
   Thoracic plate of segment 2 extending to middle of thoracic plate of segment 4 . . . . . **katoi**

Pandarus satyrus Dana, 1852

FIGURES 1–26

Pandarus satyrus Dana, 1852–3, p. 1368.—Brady, 1883, p. 134.—Bassett-Smith, 1899, p. 467.—Wilson, 1907, p. 415; 1914, p. 71.—Yamaguti, 1936, p. 5.—Bere, 1936, p. 595.—Shiino, 1957, p. 364; 1959a, p. 315; 1959b, p. 352; 1960b, p. 493.—Ho, 1963, p. 90.

SPECIMENS STUDIED.—All collections from *Prionace glauca* (Linnaeus). Twenty-six collections made in the western North Atlantic Ocean between latitudes 30°N to 49°N and longitudes 60°W to 72°W. Six collections in the Indian Ocean (0°58′N, 55°E; 0°14′S, 55°04′E; 6°37′S, 55°00′E; 34°32′S, 74°48′E; 33°11′S, 54°58′E; 02°06′S, 75°10′E. Three collection in Pacific Ocean (3°18′N, 101°54′W; 1°00′S, 101°40′W; 9°56′N, 135°16′W).

FEMALE.—Body form as in figure 1. Length 8.2 mm and width (measured at widest point) 4.4 mm based on average of 10 specimens.

First thoracic segment fused with head. Dorsal thoracic plates present on segments 2–4. Plates on segment 2 separate, extending laterally beyond tip of plate of segment 3. Plates of segment 3 fused at base, divided by a broad median distal sinus in middle of distal margin. Plates of segment 4 extending over the genital segment, fused, and with distal median sinus. Genital segment 1.8 mm long and 2.7 mm wide. Abdomen 1-segmented and joined broadly to genital segment ventrally. Abdomen covered by dorsal plate (1.8 by 1.5 mm), longer than wide, extending beyond tips of rami. Caudal rami (fig. 2) long, slender, widest at base, tapering distally (990μ by 228μ), bearing 4 short spines. Rami extend only to about middle of abdominal plate.

Oral area (fig. 3). Adhesion pads present at bases of first antennae, second antennae, and maxillipeds. Pads also present at posterior corners of cephalon. First antenna (fig. 4) 2-segmented. First segment bearing 26 setae, 4 setae small and plumose, remainder stout and armed as in figure. Second segment bearing 12 naked setae. Second antenna (fig. 5) 3-segmented. Terminal segment bearing large terminal spine and 2 setae. Mouth tube (figs. 6, 7) of usual caligoid type. Labrum with pari of subterminal processes within tube and fringed at its tip. Labium somewhat expanded at tip and with fringe as in figure 7. Mandible (fig. 8) composed of basal podomere bearing long slender shaft with serrate tip. Mandibular process extending within tube as in figure 6. First maxilla (fig. 6) 2-segmented. Basal segment bearing 3 short setae. Terminal segment with small seta and large terminal spine. Second maxilla (fig. 9) with 3 segments. Basal segment unarmed. Second segment with 2 distal spines, longer one fringed, shorter plumose. Terminal segment bearing large claw with rows of spinules and apical patch of spinules. Maxilliped (fig. 10) 2-segmented. Basal segment stout, bearing an adhesion pad. Terminal segment in shape of a claw, with 1 seta. Tip of claw bilobed, with an adhesion area that, when closed, is in contact with adhesion pad of basal segment. Legs 1–4 biramose with spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:0	0:0	I:0	0:0	VI	0
seg. 2	VI	III	X	IV	VI	II	–	–

Leg 1 (fig. 11) with both rami 2-segmented. Leg 2 (fig. 12) with both rami 2-segmented. Inner 7 spines on last segment of exopodite not articulated. Leg 3 (fig. 13) with both rami 2-segmented. Two inner spines on last segment of exopodite not articulated. Leg 4 (fig. 14) with both rami 1-segmented. Endopodite without spines. Legs 1–4 with patches of spinules and adhesion pad as in figures. Leg 5 (fig. 15) consisting of outer plumose seta and inner lobe with single terminal spine.

Egg strings long and slender, extending several times length of body, not recurved. Eggs disc shaped.

Color of adult female dark brown to black with eye spots separated as in figure 1.

MALE.—Body form as in figure 16. Length (not including setae on caudal rami) 10.3 mm and width (measured at widest point) 5.6 mm based on an average of 10 specimens. Cephalon rounded when viewed dorsally with head and first thoracic segment fused. Thoracic segments 2–4 free, without dorsal plates except for lateral winglike plates on segment 2. Genital segments 2.3 mm by 2.3 mm, with posterior corners attenuated, terminating in inwardly directed tip. Spermatophores (fig. 17) often visible through genital segment. Abdomen 2-segmented. First segment 432μ long. Second segment 576μ long. Caudal ramus (fig. 18) 1050μ by 665μ, bearing 4 long and 2 short setae. Outermost long seta 1365μ long, innermost 910μ long, and 2 median setae 1500μ long. Oral area as in female except as follows: second antenna (fig. 19) with last segment in form of large claw, not subdivided as in female; maxilliped (fig. 20) terminating in pointed claw whereas female claw terminating as spatulate tip.

Legs 1–4 biramose, each ramus of 2 segments, with spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:1	0:1	I:1	0:1	I:1	0:1
seg. 2	IV:3	3	IV:6	8	IV:5	6	IV:5	5

All setae densely plumose. Leg 1 as in figure 21. First segment of endopod with prominent inner adhesion pad. Leg 2 as in figure 22. Leg 3 (fig. 23) with bilobed outer edge on first segment of exopodite. No modified setae on last endopodite segment. Leg 4 (fig. 24) also possessing bilobed outer edge on exopodite first segment. Leg 5 (fig. 25) borne on genital segment as lateral projection with 4 setae and 1 stout terminal spine (see also fig. 16). Leg 6 (fig. 26) consisting of

single plumose seta and stout spine borne on genital segment near origin of abdomen (see also fig. 16).

Color in life whitish yellow and generally devoid of darker pigment.

Discussion.—*Pandarus satyrus* is a widely distributed copepod nearly always found associated with *Prionace glauca*. Reports in the literature of this copepod from other hosts are probably the result of misidentification of the copepod or even of the host shark. It is closely related to *Pandarus cranchii* Leach and was placed in synonymy with it by Shiino (1954). I have examined a great number of specimens of both of these species and conclude that both are valid species. The principal differences between them are discussed under the description of *Pandarus cranchii*.

This copepod is parastic on the body surface of the host and is often found in large clusters near the posterior edge of the fins. Generally the number of females far exceeds the number of males.

Pandarus cranchii Leach, 1819

Figures 27–33

Pandarus cranchii Leach 1819, p. 535.—Burmeister, 1833, p. 331.—Krøyer, 1837, p. 202.—Steenstrup and Lütken, 1861, p. 390.—Rathbun, 1884, p. 488; 1886, p. 317.—Beneden, 1892, p. 221.—Wilson, 1907, p. 403; 1908, p. 453; 1932, p. 435; 1936, p. 333.—Brian, 1908, p. 4; 1912, p. 14.—Leigh-Sharpe, 1934a, p. 27.—Pesta, 1934, p. 30.—Oorde and Schuurmans Stekhoven, 1936, p. 141.—Heegaard, 1943b, p. 27.—Barnard, 1948, p. 249; 1955, p. 258.—Capart, 1953, p. 660; 1959, p. 98.—Markevitch, 1956, p. 151.

Nogagus latreilli Leach, 1819, p. 536.

Pandarus carchariae Leach, 1819, p. 535.

Pandarus concinnatus Dana, 1852, p. 59.

Pandarus pallidus Milne-Edwards, 1840, p. 468.

Pandarus vulgaris Milne-Edwards, 1840, p. 468.

Pandarus dentatus Milne-Edwards, 1840, p. 469.—Heller, 1868, p. 206.—Thomson, 1889, p. 363.—Bassett-Smith, 1899, p. 466.

Pandarus armatus Heller, 1868, p. 202.—Thomson, 1889, p. 363.—Bassett-Smith, 1899, p. 467.—Wilson, 1907, p. 448.—Stebbing, 1910, p. 558.—Capart, 1953, p. 659.—Barnard, 1955, p. 258.

Specimens studied.—Eighteen collections from *Pterolamiops longimanus* (Poey) between latitudes 30°N to 49°N and longitudes 60°W to 72°W. Two collections from *Eulamia falciformis* (Müller and Henle) (30°49′N, 64°02′W; 57°44′N, 65°42′W). Two collections from *Eulamia obscura* (Lesueur) (34°45′N, 73°41′W; 36°42′N, 70°00′W). Ten collections from *Eulamia floridanus* (Bigelow and Schroeder) between latitudes 30°N to 49°N and longitudes 60°W to 72°W. All above collections in the North Atlantic Ocean. Indian Ocean: 8 collections from *P. longimanus* (07°17′N, 55°00′E; 02°25′N, 55°04′E; 00°14′S, 55°04′E; 06°37′S, 55°00′E; 11°08′S, 55°04′E;

12°38′S, 54°40′E; 04°09′S, 74°58′E; 03°54′N, 74°59′E). Two collections from *E. floridanus* (07°17′N, 55°00′E; 00°14′S, 55°04′E). Pacific Ocean: from *Carcharinus malpeloensis* (Fowler) (9°42′N, 85°46′W), *Carcharinus galapagensis* (14°3′N, 92°8′W) and *Sphyrna zygaena* (Linnaeus) off Formosa. Also 1 collection from *P. longimanus* from Durban, South Africa, and 4 collections from this host in the Gulf of Mexico. Two collections from *Galeocerdo cuvier* (Lesueur), 1 from Formosa and the other from Pointe Noire, West Africa.

Female.—Body form as in figure 27. Length 8.4 mm and width (measured at the widest part) 4.6 mm. Based on an average of 10 specimens.

In general, dorsal view and arrangement of thoracic plates of female is same as *P. satyrus* with the following exception: caudal ramus (fig. 28) of *P. cranchii* always extends to distal tip of abdominal plate and often even beyond while ramus of *P. satyrus* is much shorter in relation to abdominal plate (see fig. 2). Ramus of *P. cranchii* measures 1.4 mm in length.

Oral area as in *P. satyrus* except that maxilliped (fig. 29) of *P. cranchii* possesses a larger basal segment. Leg 1–4 with spine and setal formula as *P. satyrus*. Endopodite of leg 2 of *P. cranchii* (fig. 30) with patch of more rugose spines along outer edge than that of *P. satyrus*. Leg 5 (fig. 31) as in *P. satyrus*. Eggs and egg strings as in *P. satyrus*.

Color as in *P. satyrus*.

Male.—Body form as in *P. satyrus*. Total length 10.4 mm. Greatest width 5.2 mm, based on an average of 10 specimens. Male of *P. cranchii* differs from *P. satyrus* as follows: second antenna of *P. cranchii* (fig. 32) with smaller claw; posterior corners of genital segment of *P. cranchii* attenuated but not curved inwardly as in *satyrus* (see fig. 33).

Discussion.—This copepod appears to be closely related to *P. satyrus* but the two species are easily separated on the basis of the caudal rami. The rami of *P. cranchii* extend at least to the tip of the abdominal plate (often beyond) whereas the rami of *P. satyrus* extends only about half the length of the abdominal plate. The legs of *P. cranchii* have the same spine and setal formula but the patches of spinules are much heavier in *P. cranchii*.

Pandarus cranchii seems to be confined primarily to carcharinid sharks. It is also common on the tiger shark, *Galeocerdo cuvier*. The parasite is found on the body surface of the host and like other members of the genus is sometimes found in large clusters on the fins. It is worldwide in distribution.

Shiino (1954) has described and figured both sexes of this species under the name of *P. satyrus*.

Pandarus smithii Rathbun, 1886

FIGURES 34–35

Pandarus smithii Rathbun, 1886, p. 315.—Wilson, 1907, p. 410; 1932, p. 158.—Leigh-Sharpe, 1934, p. 27.—Bere, 1936, p. 595.—Carvalho, 1940, p. 281; 1945, p. 110; 1951, p. 139.—Brian, 1944, p. 202.—Barnard, 1948, p. 249; 1955, p. 259.—Causey, 1955, p. 6.—Shiino, 1959b, p. 353.

Pandarus lugubris Heller, 1868, p. 205.—Bassett-Smith, 1899, p. 467.—Brian, 1902, p. 8; 1906, p. 56.—Wilson, 1907, p. 395.—Rose and Vaissiere, 1953, p. 86.

Pandarus marcusi Carvalho, 1940, p. 284; 1951, p. 140.

SPECIMENS STUDIED.—Two collections from *Isurus oxyrhynchus* Rafinesque (42°18′N, 64°02′W; 35°00′N, 70°00′W). Two collections from *Eulamia obscurus* (Lesueur) (36°42′N, 70°00′W; 34°45′N, 73°41′W). Three collections from *Eulamia floridanus* Bigelow and Schroeder (36°07′N, 73°25′W; 38°00′N, 68°00′W; 40°25′N, 62°35′W). All above in North Atlantic Ocean. From the Indian Ocean 2 collections from *Alopias vulpinus* (Bonneterre) (9°24′N, 54°58′E; 07°17′N, 55°00′E). Single collections from *Isurus oxyrhynchus* (16°13′N, 63°29′E) and *Eulamia floridanus* (07°17′N, 55°00′E). From the Pacific Ocean 2 collections from *Carcharinus azureus* (9°52′N, 85°29′W; 10°09′N, 86°04′W). Single collections from *Carcharinus galapagensis* (9°45′N, 85°34′W), *Carcharinus malpeloensis* (Fowler) (Très Madres Island), *Carcharinus limbatus* Müller and Henle, off San Pedro, Calif. Also single collections from *Hypoprion signatus* Poey in the Gulf of Mexico, *Carcharodon carcharias* (Linnaeus) off Cape Cod, Mass., and *Sphyrna zygaena* (Linnaeus) off the coast of Brazil.

FEMALE.—Body form as in figure 34. Length 8.2 mm and width 4.6 mm based on an average of 10 specimens. Dorsal thoracic plates similar to those of *P. satyrus* and *P. cranchii* except that plates of segment 2 extend only to about middle of plate of segment 4. Genital segment 2.2 mm long and 3.0 mm wide. Abdomen 1-segmented as in *P. satyrus*. Dorsal plate of abdomen nearly round (see fig. 35). Caudal rami (figs. 35, 36) 1.78 mm long and with an inner lobe extending ventrally below abdomen. In some specimens lobes extending toward midline almost touching and thus forming shelflike structure bridging the rami.

Oral area similar to that of *P. satyrus*. Second antenna (fig. 37) and maxilliped (fig. 38) are illustrated to show minor differences in shapes of segments and lengths of spines. Legs 1–4 modified as in *P. satyrus* and with the following spine and setal formula:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	1:0	0:0	I:0	0:0	VI	I or 0
seg. 2	VI	III	X	IV	VI	I or II		

Formula like that of *P. satyrus* and *P. cranchii* except in variation of numbers of spines on last podemere of expodite of legs 3 and 4 (fig. 39).

Leg 5 (fig. 40) with inner lobe in form of large claw. Egg strings as in other *Pandarus* species. Color dark brown to black in pigmented areas (see fig. 34). Eye spots joined at midline and not separated as in *P. satyrus*.

MALE.—Body form as in figure 41. Length 9.4 mm (not including setae on caudal rami) and width (measured at widest point) 4.4 mm based on an average of 10 specimens. General configuration similar to other *Pandarus* species. Genital segment (fig. 42) 2.0 mm by 1.8 mm with posterior corners not produced as in *P. satyrus* and *P. cranchii*. Spermatophore visible through genital segment. Oral area as in *P. satyrus*. Legs 1.4 biramose with spine and setal formula as in *P. satyrus*. Leg 1 (fig. 43) showing minor differences in adhesion areas and length of setae when compared with *P. satyrus*. Leg 2 (fig. 44) with papillose area on outer corner of coxopodite rather than patch of fine setules as in *P. satyrus*. Leg 5 (fig. 45) with 3 plumose setae and 1 small spine and borne laterally on genital segment as in *P. satyrus*. Leg 6 consisting of 1 short spine and a single seta located at junction of genital segment and abdomen.

Color in life whitish yellow and generally devoid of darker pigment.

DISCUSSION.—*Pandarus smithii* is a widely distributed copepod found on a number of hosts and often occurring with *Pandarus cranchii* on carcharinid sharks. *P. smithii* can be easily distinguished from the other species of the *cranchii* group on the basis of the caudal ramus and eye spots in pigmented females. Males can be separated from *cranchii* and *satyrus* on the basis of the shape of the genital segment and nature of leg 5.

In 1940 Carvalho described a new species, *Pandarus marcusi*. I have examined material identified by Carvalho as this new species from Brazil and have concluded that it is in fact a synonym of *P. smithii*. The sole basis for separating *marcusi* from *smithii* was the shape of the dorsal plate of the abdomen. *P. marcusi* had a plate with a deep median sinus. This irregularity in the shape of plates is not uncommon in the genus. I have observed these irregularities in collections of *Pandarus* that show an epiphyte (algal or fungal) growing on the surface of the copepod. The "roots" of the epiphyte seem to have a corrosive action on the integument and often leave the area malformed.

Pandarus floridanus, new species

FIGURES 46–66

SPECIMENS STUDIED.—Thirty-two females and 1 male collected from *Carcharodon carcharias* (Linnaeus) caught at Dennis, Mass. Holotype female, allotype male, and 10 paratype females in alcohol deposited in the U.S. National Museum, 10 paratype females in

alcohol deposited in the British Museum (Natural History) and the remaining paratypes in the author's collection. Other specimens studied: 3 collections from *Carcharodon carcharias* (USNM 107299, Miami, Fla.) (USNM 101876, off Cape Lookout, N.C.) (USNM 104859, St. Augustine, Fla.); a single collection (USNM 32765) from *Lamna nasus* (Bonneterre) Woods Hole, Mass.

FEMALE.—Body form as in figure 46. Total length (based on an average of 5 specimens) 7.5 mm. Greatest width (measured at widest part of cephalon) 3.8 mm. Cephalon widest posteriorly narrowed anteriorly, measuring 3.5 by 3.8 mm. First thoracic segment fused to head. Dorsal thoracic plates present on segments 2–4. Plates of segment 2 extending well beyond those of segment 3 to about middle of lateral edge of plate of segment 4. Plates of segments 3 and 4 fused at bases. Genital segment nearly square measuring 2.8 mm long and 2.6 mm wide. Dorsal posterior border of genital segment has broad sinus to accommodate dorsal abdominal plate. Abdomen 1-segmented with a dorsal plate (see fig. 47) slightly wider than long (7.9 by 7.2 mm). Caudal ramus of usual generic type, bearing 4 setae (see fig. 47) and 0.6 mm long.

Oral area as in figure 48. First antenna 2-segmented. First segment 490μ long bearing 25 spines and setae. Spines and setae armed as in the figure. Second segment 168μ long bearing 11 naked setae. Second antenna (fig. 48) 3-segmented. Terminal segment in form of claw and bearing 2 spines. Mouth tube with associated mandible and first maxilla as in other members of genus. Second maxilla with usual fringed clawlike tip. Short plumose seta (fig. 49) near base of terminal segment. Maxilliped of the usual type (see fig. 48).

Head appendages, except maxilliped, as in female. Maxilliped with distinct claw at tip as in *P. satyrus* (see fig. 20).

Legs 1–4 not modified as in female and with spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:1	0:1	I:1	0:1	I:1	0:1
seg. 2	IV:3	3	IV:6	8	IV:5	6	IV:5	5

Legs 1–4 biramose and each ramus 2-segmented. All setae plumose. Leg 1 (fig. 61) with adhesion pads as indicated in figure. Leg 2 (fig. 62) exopod with first segment bearing long hairs along outer edge and outer distal corner. Leg 3 (fig. 63) with no modifications for holding on last endopod segment. Leg 4 as in figure 64. Leg 5 (fig. 65) consisting of 3 short plumose setae and one short, stout spine located on midlateral margin of genital segment. Leg 6 (fig. 66) located at junction of genital segment and abdomen, consisting of a spinelike process with stout plumose seta near base.

Color in life cream and generally devoid of pigmentation.

Legs 1–4 biramose, with spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:0	0:0	I:0	0:0	VI	0
seg. 2	VI	III	IX	V	VI	II		

Leg 1 (fig. 52) with both rami 2-segmented. First exopod segment with outer spine. Last exopod segment with 6 spines, outer 3 naked, inner 3 finely plumose. First endopod segment with adhesion pad. Last endopod segment with 3 inner spines. Basipod having an inner and outer spine with 1 adhesion pad. Leg 2 (fig. 53) with both rami 2-segmented. First exopod segment with 1 outer spine and patch of fine spinules on outer distal half. Last segment with 9 spines, outer 4 spinose and inner 5 naked. First endopod segment unarmed. Second endopod segment with 5 short spines at tip. Leg 3 (fig. 54) with both rami 2-segmented. First exopod segment with spine on outer distal corner. Second segment with 6 short spines. First endopod segment unarmed. Second segment with 2 short terminal spines. Leg 4 (fig. 55) with both rami 1-segmented. Exopod segment with 6 spines. One spine placed at midpoint of outer edge suggesting a 2-segmented ramus. Endopod unarmed. Leg 5 (fig. 56) consisting of naked spine and separate plumose seta. Leg 5 located near point of attachment of spermatophores (see fig. 56). Area of spermatophore attachment located at junction of abdomen to genital segment and composed of a heavily sclerotized area with shelf to receive neck of spermatophores, attaching in these areas with necks crossing to opening of seminal receptacle on opposite side. Egg strings long and of usual generic type.

Color in life creamy yellow with light brown pigmentation as indicated in figure 46.

Male.—Body form as in figure 57. Total length based on 1 specimen, 9.5 mm, including caudal ramus but not setae. Greatest width 4.5 mm, measured at widest part of cephalon. Cephalon rounded, slightly longer than wide (4.9 by 4.4 mm).

First thoracic segment fused with head. Segments 2–4 free without dorsal plates. Genital segment longer than wide, 2.2 by 1.7 mm with spermatophore visible within. Abdomen of 2 segments. First segment 360μ long. Second segment 612μ long. Caudal ramus (fig. 58) bearing 6 setae, inner 4 long and plumose, inner margin of caudal ramus bearing row of hairs.

Oral area similar to that of female. In adult male adhesion pad associated with second antenna only about one-half length of pad of first antenna (264:576μ) (see fig. 59). Collected with this mature male was also a young male (7.1 mm) with spermatophores developing

within genital segment (by itself, this might have been mistaken for fully developed male). Examination of its appendages showed it to be identical with its larger counterpart, except pad of second antenna is about as long as pad of first antenna (408:420μ) (see fig. 60). Other species of this genus with same reduction of adhesion pad of second antenna in mature males.

Discussion.—*Pandarus floridanus* is closely related to *P. sinuatus* but the females can be readily separated on the basis of the following differences. The dorsal abdominal plate of *P. floridanus* is considerably longer than the dorsally exposed caudal ramus while in *P. sinuatus* they are about equal in length (see table 1). In *P. floridanus* the

Table 1.—Comparison of the length of the dorsal abdominal plates with the length of dorsally exposed caudal ramus in some specimens of *Pandarus floridanus* with *P. sinuatus* (CHML=Cape Haze Marine Laboratory, Fla.)

Specimens	Plate	Ramus
P. floridanus		
ex *Carcharodon carcharias* (avg. of 4) Dennis, Mass.	702μ	450μ
" " (avg. of 2) USNM 107299	810μ	576μ
" " (1 spec.) USNM 101876	720μ	540μ
ex *Lamna cornubica* (1 spec.) USNM 32765	720μ	360μ
P. sinuatus		
ex *Negaprion brevirostris* (avg. of 2) CHML	495μ	468μ
ex *Carcharinus leucas* (avg. of 2) CHML	621μ	630μ

dorsal thoracic plate of segment 2 extends beyond the middle of the plate of segment 4 while in *P. sinuatus* the plate of segment 2 does not extend to the middle of the plate of segment 4. *P. floridanus* is not so heavily pigmented as *P. sinuatus*. Young females of *P. sinuatus* first show pigmentation in the lateral areas of the cephalon (see fig. 66), whereas *P. floridanus* is not pigmented in this area at all (its young females showing first areas of pigmentation to be the anterior margin of the cephalon).

From Latin, the word *floridanus* refers to the fact that the species was seen first on a shark from Florida.

Pandarus floridanus can be separated from all other species of the *cranchii* group on the basis of the spine and setal formula. The male of *P. floridanus* is similar to that of *P. sinuatus*. Since only 1 mature male of the new species was available, a more detailed comparison could not be made.

This species seems to be a well-established parasite on the body surface of *Carcharodon carcharias* since it was recovered from that host

on four different occasions in the Western Atlantic. It should also be noted as having been collected from *Lamna nasus* as well.

Pandarus sinuatus Say, 1817

FIGURES 67, 68

Pandarus sinuatus Say, 1817, p. 436.—Milne-Edwards, 1840, p. 470.—Smith, 1874, p. 283.—Rathbun, 1886, p. 310.—McClendon, 1906, p. 44; 1907, p. 114; 1910, p. 229.—Wilson, 1907, p. 417; 1932, p. 437.—Bere, 1936, p. 595.—Carvalho, 1940, p. 283; 1945, p. 111; 1951, p. 139.—Pearse, 1952a, p. 27; 1952b, p. 213.—Causey, 1953, p. 12; 1955, p. 6.

Pandarus affinis Beneden, 1892a, p. 224.—Bassett-Smith, 1899, p. 467.—Wilson, 1907, p. 394.—Capart, 1953, p. 660.

SPECIMENS STUDIED.—Two collections from *Carcharinus leucas* Müller and Henle from Sarasota, Fla. From the same locality a single collection from *Negaprion brevirostris* (Poey). In addition to these, I examined 88 collections from the U.S. National Museum collected at various localities along the eastern coast of the United States. These collections are from a wide variety of shark hosts generally restricted to inshore species.

FEMALE.—Body form as in figure 67. Total length (based on an average of 5 specimens) 6.5 mm. Greatest width (measured at widest part of cephalon) 3.2 mm. Appendages of this species inseparable from those of *P. floridanus* except last segment of exopod of leg 2 bears 10 spines instead of 9 as in *P. floridanus*. Since a description of appendages of this species would only duplicate that of *P. floridanus*, none will be given here. Only those features that separate it from *P. floridanus* will be emphasized.

Dorsal plate of segment 2 extending only to anterior third of plate of segment 4. Abdominal plate small and rounded, only about as long as exposed caudal ramus (see table 1). Color dark brown to black with eye spots fused and continuous with median unpigmented line from posterior edge of eye spots to posterior margin of cephalon. Young females (fig. 68)with pigment first developing in lateral areas of cephalon.

MALE.—As in *P. floridanus*.

DISCUSSION.—*P. sinatus* is apparently found only on sharks inhabiting coastal waters of the western North Atlantic Ocean. It occurs only on the body surface of the host usually in clusters on the fins as do other members of the genus. It is closely related to *P. floridanus* but is easily separated from it on the basis of the above characteristics. Superficially, this copepod also may be confused with *P. bicolor* because of the pigmentation, but it can be easily distinguished from this species on the basis of the thoracic plates. The dorsal plates of segment 2 of *P. bicolor* do not extend beyond the plate of segment 3.

***Pandarus katoi*, new species**

FIGURES 69–96

SPECIMENS STUDIED.—Thirty females and 10 males from *Carcharinus malpeloensis* (Fowler) from the Pacific (09°55′N, 85°51′W). Holotype female, allotype male, and 14 paratypes (10♀ ♀ and 4♂ ♂) in alcohol deposited in the U.S. National Museum. Fourteen paratypes (10♀ ♀ and 4♂ ♂) deposited in the British Museum (Natural History) and the remaining paratypes in the author's collection. Additional specimens studied: 4 collections from *C. malpeloensis* from the Pacific Ocean (09°42′N, 85°51′W; 21°20′N, 106°50′W; 10°03′N, 85°53′W; 08°25′N, 83°45′W), 2 collections from *C. azureus* from the Pacific (9°52′N, 85°29′W; 10°09′N, 86°04′W), and a single collection from the Cocos Islands from *C. platyrhynchus*.

FEMALE.—Body form as in figure 69. Total length (based on an average of 5 specimens) 5.6 mm. Greatest width (measured at the widest part of the cephalon) 3.8 mm. Cephalon somewhat rounded, 3.0 by 3.8 mm. First thoracic segment fused to head. Dorsal thoracic plates present on segments 2–4. Plates of segment 2 extending beyond those of segment 3 and to about middle of plates of segment 4. Plates of segment 2 are generally slightly divergent. Plates of segments 3 and 4 fused at their bases. Genital segment 2.3 by 2.3 mm. Abdomen 1-segmented (fig. 70), with dorsal plate. Dorsal plate 3.0 by 2.3 mm, slightly longer than wide. Caudal ramus (see fig. 70) 720μ long and 270μ wide bearing 4 spines and 2 plumose setae.

Oral area as in other members of genus. Adhesion pads associated with first antennae, second antennae, maxillipeds, and a pair at ventral distal corners of cephalon. First antenna (fig. 71) 2-segmented. First segment 600μ long and bearing 13 naked setae (fig. 72). Second antenna (fig. 73) 3-segmented. Terminal segment with 2 spines, in form of stout claw. Figure 73 shows adhesion pad (dotted line) in relation to second antenna. Mouth tube of typical pandarid type. Mandible (fig. 74) within tube. First maxilla (fig. 75) with a terminal claw, 3 short setae, and located near base of mouth tube. Second maxilla (fig. 76) armed as in figure. Maxilliped (fig. 77) terminal claw with spatulate tip and opposed by 1 large adhesion pad on basal segment.

Legs 1–4 biramose, with spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:0	0:0	I:0	0:0	VII	I
seg. 2	VI	III	X	IV	VI	II		

Leg 1 (fig. 78) with both rami 2-segmented. First exopod segment with outer fringed spine. Last exopod segment with 6 terminal spines. First endopod segment with adhesion pad. Last endopod

segment with 3 inner spines. Leg 2 (fig. 79) with both rami 2-segmented. First exopod segment with outer spine. Last exopod segment with 10 spines (outer 4 articulated, inner 6 not). First endopod segment unarmed. Last endopod segment with 4 naked spines. Leg 3 (fig. 80) with both rami 2-segmented. First exopod segment with outer spine. Last exopod segment with 6 spines. First endopod segment unarmed. Last endopod segment with 2 terminal spines (all spines on rami of leg 3 naked). Leg 4 (fig. 81) with both rami 1-segmented. Exopod with 7 spines. Endopod with 1 short spine. All spines naked. Leg 5 (fig. 82) with outer single spine and inner lobe with 3 spines. Leg 5 located near point of attachment of abdomen (see fig. 70). Area of attachment of spermatophore at junction of abdomen and genital segment, composed of a heavily sclerotized area with shelf to receive neck of spermatophore. Spermatophores crossing with neck penetrating opening of the seminal receptacle of opposite side. Egg strings long and composed of single strands of eggs.

Color in life creamy yellow with light brown pigmentation as in figure 69.

MALE.—Body form as in figure 83. Total length, based on 5 specimens, 7.4 mm. Greatest width 4.2 mm measured at widest part of cephalon. First thoracic segment fused with head. Segments 2–4 free and without dorsal plates. Genital segment somewhat longer than wide, 1.98 by 1.72 mm with spermatophores visible within. Abdomen 2-segmented. First segment 300μ long. Second segment 410μ long. Caudal ramus (fig. 84) with 6 setae, the inner 4 long and plumose. Inner margin of caudal ramus bearing row of hairs.

Oral area similar to that of female. As in *P. floridanus*, adhesion pad of second antenna considerably smaller than one associated with first antenna (204:516μ) (see fig. 85). First antenna (fig. 86) as in female except spines more heavily barbed. Second antenna (fig. 87) 4-segmented with adhesion pad on basal segment. Terminal segment in form of claw with 2 median spines. Mouth tube and mandible as in female. First maxilla (fig. 88) similar to that of female except terminal claw has a more striated surface. Second maxilla (fig. 89) as in female. Maxilliped (fig. 90) with terminal claw pointed rather than spatulate as in female. Opposing adhesion area composed of 3 pads instead of 1 as in female.

Legs 1–4 not modified as in female and with spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:1	0:1	I:1	0:1	I:1	0:1
seg. 2	IV	3	III:6	8	IV:5	6	IV:5	5

Legs 1–4 biramose and each ramus 2-segmented. All setae plumose. Leg 1 (fig. 91) with adhesion areas as in the figure. Leg 2 (fig. 92)

with outer edge of exopod first segment with long hairs and short spinules. Leg 3 (fig. 93) with outer edge of exopod first segment bilobed. Leg 4 (fig. 94) with outer edge of exopod first segment similar to that of leg 3. Leg 5 (fig. 95) situated on midlateral margin of genital segment and consisting of a lobe bearing 4 spines, 1 naked and 3 smaller and plumose. Leg 6 (fig. 96) situated at point of attachment of abdomen to genital segment and consisting of lobe bearing 3 spines (1 plumose and 2 naked). Color in life cream, generally devoid of pigment.

DISCUSSION.—This species thus far has been collected only from carcharinid sharks of the western central Pacific Ocean. It is closely related to *P. zygaenae* but can be separated from this species by the nature of the dorsal thoracic plates. The plates of the second thoracic segment of *P. katoi* extend only to about the middle of the plate of the fourth segment, whereas in *P. zygaenae* these plates extend to the distal end of the plate of segment 4. Since the appendages of these 2 species are identical, it seems probable that they have evolved from a common ancestor and thus are very closely related. Because I was able to examine several collections of each species (10 collections of *P. katoi*, 4 collections of *P. zygaenae*), a good sample for comparison was available. In each case the copepods are separated easily on the aforementioned characters.

I have named this species for Mr. Susumu Kato, who originally collected the type material and who has generously collected in the Pacific area for me.

Pandarus zygaenae Brady, 1883

FIGURES 97–99

Pandarus zygaenae Brady, 1883, p. 134.—Bassett-Smith, 1899, p. 467.—Wilson, 1907, p. 416.

SPECIMENS STUDIED.—Collections from the following areas: Off São Paulo, Brazil, from *Sphyrna zygaena* (Linnaeus); Pacific (9°47′ N, 85°48′ W) from *Sphyrna* species; Pacific (18°31′ N, 109°34′ W) from *Sphyrna zygaena*.

FEMALE.—Body form as in figure 97. Total length (based on an average of 2 specimens) 7.6 mm. Greatest width (measured at the widest part of the cephalon) 3.9 mm. Cephalon somewhat truncated and measuring 3.7 by 3.9 mm, somewhat wider than long. Thoracic plates present on segments 2–4. Plates of segment 2 extending beyond those of segment 3 and to distal border of plate of segment 4. Genital segment somewhat longer than wide (2.7 by 2.3 mm). Abdomen 1-segmented and with dorsal plate. Caudal rami as in *P. katoi* except that they are generally held parallel to each other.

Oral area and all appendages like those of *P. katoi* with the follow-

ing 2 exceptions: tip of maxilliped of *P. zygaenae* (fig. 98) shaped somewhat differently; endopod of *P. zygaenae* unarmed; spine and setal formula, otherwise, same as *P. katoi.*

Color in preserved material creamy white except for some light brown pigmentation in mature females as indicated in figure 97.

MALE.—Body form as in figure 99. Male indistinguishable from male of *P. katoi.* Only 1 male of each species was collected. More material of both species might show some differences between the males of these 2 species. Total length of male of *P. zygaenae* (based on a single specimen) 8.1 mm (length not including setae on caudal rami). Greatest width 4.6 mm.

DISCUSSION.—Brady described this species in 1883 from *Zygaena malleus* collected near Cape Verde Islands. In 1907 Wilson placed the species in synonomy with *Pandarus satyrus.* Wilson examined 2 females from Brady's original collection but noted that the copepods were so covered with "fish slime" as to be difficult to study. I received 2 collections of copepods from the same host with enough material to ascertain that these were not *P. satyrus* but clearly a separate species. A comparison of this new material with Brady's original description and figures prove his species to be valid. The figure of the female by Brady appears to be of an immature form but shows some features consistent with my recent collections, namely, the relative lengths of the dorsal thoracic plates and the fact that the caudal rami are generally held parallel to each other rather than divergent as in most other members of the genus (in preserved specimens).

This species is closely related to *P. katoi* but can be distinguished from it by the relationship of the plates of segment 2 to those of segment 4. *P. zygaenae* so far has been found only on the genus *Zygaena* and may well be confined to species of hammerhead sharks.

Pandarus bicolor Leach, 1816

FIGURES 100–108

Pandarus bicolor Leach, 1816, p. 405; 1819, p. 535.—Desmarest, 1825, p. 339.—Burmeister, 1833, p. 331.—Krøyer, 1837, p. 202; 1838, p. 34; 1863, p. 261.—Milne-Edwards, 1840, p. 470.—Baird, 1850, p. 288.—Beneden, 1851a, p. 94; 1861, p. 148.—Norman, 1868, p. 301.—Olsson, 1868, p. 21.—Richiardi, 1880, p. 149.—Carus, 1885, p. 362.—Bassett-Smith, 1896, p. 156; 1899, p. 466.—Brian, 1898a, p. 12; 1899, p. 3; 1906, p. 55; 1914b, p. 7; 1940, p.11.—Scott, T., 1900, p. 157.—Scott, A., 1904, p. 40.—Norman and Scott, T., 1906, p. 211.—Wilson, 1907, p. 400; 1932, p. 436; 1935b, p. 778.—Scott, T., and Scott, A., 1913, p. 95.—Hansen, 1923, p. 36.—Scott, A., 1929, p. 95.—Leigh-Sharpe, 1934b, p. 112.—Pesta, 1934, p. 29.—Oorde and Schuurmans Stekhoven, 1936, p. 141.—Stephensen, 1940, p. 5.—Rose and Vaissiere, 1953, p. 86.—Barnard, 1955, p. 257.—Nunes-Ruivo, 1956, p. 17.—Causey, 1960, p. 331.—Heegaard, 1962, p. 177.

Pandarus boscii Leach, 1816, p. 406; 1819, p. 535.—Guérin-Meneville, 1829–1843, p. 41.—Burmeister, 1833, p. 331.—Desmarest, 1825, p. 339.—Krøyer, 1837, p. 202.—Baird, 1850, p. 289.
Caligus bicolor.—Lamarck, 1818, p. 137.
Pandarus fissifrons.—Milne-Edwards, 1840, p. 470.
Pandarus lividus.—Frey and Leuckart, 1847, p. 166.

SPECIMENS STUDIED.—Three collections of females from *Squalus acanthias* Linnaeus caught at the following locations: in the North Sea, eastern North Atlantic (53°04′ N, 04°02′ E), and off the coast of the Netherlands.

FEMALE.—Body form as in figure 100. Total length (based on an average of 2 specimens) 9.1 mm. Greatest width (measured at the widest part of the cephalon) 3.8 mm. Cephalon only about one-third body length, measuring 3.6 by 3.8 mm. Dorsal thoracic plates present on segments 2–4. Plates of segment 2 short and not extending beyond the posterior edge of plates of segment 3. Plate of segment 4 fully exposed. Abdomen 1-segmented (see fig. 101) and covered by broad dorsal plate. Caudal ramus (fig. 101) broad and much shorter than in other species of genus. Caudal rami not obvious in dorsal view. Each ramus armed with 5 short spines.

Oral area as in other members of genus. Since this species has been well reported and amply figured in the literature, only salient features included here. Second antenna (fig. 102) with short claw at tip separated from last segment. In other species of genus these 2 elements are often fused. Maxilliped (fig. 103) with spatulate process at tip of claw.

Legs 1–4 biramose with spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:0	0:0	I:0	0:0	VI	I
seg. 2	VI	III	VIII	V	VI	II		

Legs not notably different from other species of genus with exception of reduction in number of spines on last segment of exopod of leg 2 (8 instead of 10) and elongated nature of exopod of leg 4. Legs 1–4 as in figures 104–107. Leg 5 (fig. 108) with outer single spine and inner lobe with 3 spines.

Color cream yellow to dark brown in pigmented areas. Cephalon usually heavily pigmented with eye spots not separated and often joined by median clear stripe extending distally.

MALE.—No material available for study. Apparently male of this species is rare, as no collection examined contained one. It is interesting to note that males of *P. carcharini* and *P. niger* (probably closely related to *P. bicolor*) are unknown.

T. and A. Scott (1913) illustrate male of *P. bicolor* and their figures show it to be much the same as other males of the genus.

Spine and setal formula (based on T. and A. Scott's illustrations) are as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:1	0:1	(not illustrated by the Scotts)			
seg. 2	IV:3	3	IV:6	8				

Remarks.—This copepod seems to be limited to the waters of the eastern Atlantic and is the primary species of *Pandarus* found in the coastal waters of Europe. It seems to be restricted to smaller inshore species of sharks and, as far as recorded in the literature, is found only on the body surface of its host.

Pandarus bicolor can be easily separated from the other known species of the genus on the basis of the caudal rami. The relative lengths of the dorsal thoracic plates of segments 2 and 3 separate it from all species of the *cranchii* group. This copepod has twice been confused by American authors (Wilson, 1932, and Causey, 1960) with *P. sinuatus* because of the presence of a median stripe from the eye spots to the distal border of the cephalon of both species. I have examined specimens in the U.S. National Museum identified by Wilson as *P. bicolor* and they are clearly *P. sinuatus*.

Finally, I have placed *Pandarus lividus* Frey and Leuckart in synonymy with *P. bicolor*. Wilson (1907) commented that it was impossible to separate the 2 species on the basis of Frey's and Leuckart's description but he did not place it in synonymy. Frey and Leuckart gave no figures of *P. lividus*.

Pandarus niger Kirtesinghe, 1950

Figures 109–118

Pandarus niger Kirtesinghe, 1950, p. 83.

Specimens studied.—A female paratype loaned to me by Kirtesinghe, and a single collection of 6 females from *Galeorhinus* species in Formosa.

Female.—Since this species has been described recently by Kirtesinghe (1950), I will be concerned with only those features taxonomically important to the genus. Body form as in figure 109. Total length 8.2 mm (based on an average of 2 specimens). Greatest width (measured at the widest part of the cephalon) 3.8 mm. Cephalon somewhat truncated only about one-half as wide across anterior third as across posterior third. First thoracic segment fused to head. Dorsal thoracic plates present on segments 2–4. Plates of segments 2 and 3 fused basally with posterior borders more or less in a straight line across proximal portion of plate of segment 4. Plate of segment 4 with posterior border nearly straight with only a very slight medial indentation. Genital segment as in other species of genus. Abdomen

1-segmented and with dorsal plate. Dorsal plate small, extending only slightly beyond posterior border of abdomen (see fig. 110). Caudal ramus (fig. 110) long (1.8 mm) and well exposed dorsally.

Oral area as in other members of genus. First antenna (fig. 111) 2-segmented, bearing 22 spines on first segment and 10 naked setae on second segment. Second antenna (fig. 112) with tip produced into a short claw similar to that of *P. bicolor*. First maxilla (fig. 113) with group of short spines on basal third composed of only 2 spines rather than usual 3. Second maxilla (fig. 112) with distal setae in form of fringed claw.

Legs 1–4 (figs. 115–118) biramose and with spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:0	0:0	I:0	0:0	VII	II
seg. 2	VI	III	X	VII	VI	III		

Leg 5 (see fig. 110) with an inner lobe and an outer long seta.

Color dark brown except where unpigmented. Eye spots separated in older females.

MALE.—Unknown. Kirtesinghe (1950) illustrates and briefly describes an immature male but not enough is shown to be of value in an analysis of the adult.

REMARKS.—So far this copepod has not been reported from areas other than Ceylon and Formosa. It may well be a parasite restricted to the Indian Ocean and western Pacific. Not enough is known to ascertain its host preferences but inshore carcharinid sharks seem to be preferred hosts.

This copepod is closely related to *P. bicolor*, but the nature of the caudal ramus separates it easily from all other members of the genus. Kirtesinghe (1950) notes the relationship between this species and *P. bicolor;* he also suggests an affinity with *P. satyrus* on the basis of the caudal ramus. A comparative survey of the genus shows this not to be so, especially on that basis since the caudal ramus of *P. satyrus* does not extend beyond the tip of the abdominal plate.

Pandarus carcharini Ho, 1960

FIGURES 119–124

Pandarus carcharini Ho, 1963, p. 93.

SPECIMENS STUDIED.—Paratype female from Formosa loaned to me by Ho. Also 2 more collections of females from Formosa from *Galeorhinus* species and *Carcharinus gangeticus*. Three collections from Nosy Bé, Madagascar, from *Carcharinus leucas*, *C. sorrah*, and *C. limbatus*. A single collection from Durban, South Africa, from *C. leucas*.

FEMALE.—A full description of this species will not be given here since it has been well described recently by Ho (1960). Body form as in figure 119. Total length 9.8 mm (based on an average of 3 specimens). Greatest width 4.9 mm (measured at the widest part of the cephalon). Cephalon somewhat truncated but not as narrowed anteriorly as *P. niger*. First thoracic segment fused with head. Dorsal thoracic plates on segments 2–4 with plates of segments 2 and 3 fused basally, posterior borders forming a straight line as in *P. bicolor* and *P. niger*. Some of the salient features have been figured for the sake of comparison. Caudal rami (fig. 120) intermediate between that of *P. bicolor* and *P. niger*, measuring 1.26 mm in length and extending posteriorly only about as far as the dorsal abdominal plate.

Oral area as in *P. niger*. Appendages of cephalon as in *P. niger* except that first antenna (fig. 121) has 24 spines on first segment and 10 naked setae on last.

Legs 1–4 biramose, with spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:0	0:0	I:0	00:	VIII	I
seg. 2	VI	III	X	VI	VII	II		

Legs 2–4 as in figs. 122–124. Leg 5 as in *P. niger*.

Color creamy yellow with dark brown pigmentation as in figure 119. Eye spots fused. Egg strings of usual type.

MALE.—Unknown.

REMARKS.—This species described by Ho (1960) from Formosa has been collected by the author in Nosy Bé, Madagascar, from carcharinid sharks. Its range may well be the same as *P. niger* but not enough material has been collected on which to base a definitive conclusion; nevertheless, from what is known, it appears to be a parasite of inshore species of sharks in the Indian Ocean and western Pacific coast.

Pandarus carcharini may be separated from its closely related species (*P. bicolor* and *P. niger*) on the basis of the caudal ramus and the spine and setal formula. Ho (1960) has already cited the similarities between those 3 species. His comparison and description implies the presence of a ventral abdominal plate. I could find no evidence of a ventral plate and, after personal communication with Ho, he agrees that this is synonomous with the abdomen and that the use of the term "plate" is invalid in this case.

Genus *Phyllothereus* Norman 1903

Phyllophora Milne-Edwards, 1840, p. 471. [Type-species: *P. cornutus*.]
Nogagus.—Steenstrup and Lutken, 1861, p. 386. [Refers to *N. grandis* only.]
Laminifera Poche, 1902. [Cite Wilson, 1907, p. 361.]

Phyllothereus Norman, 1903, p. 368.
Parapandarus Wilson, 1924a, p. 7.

FEMALE.—Frontal plate distinctly separate. First thoracic segments 2–4 free and possessing dorsal plates. Dorsal plate of segment 3 extending well beyond distal margin of plates of segment 2. Plates of segment 4 separated. Abdomen 1-segmented and with a dorsal plate. Abdomen or its plate visible dorsally and attached to distal end of genital segment. Caudal rami lateral to abdomen. First antenna 2-segmented. Claw of maxilliped pointed at tip. Adhesion pads absent or much reduced. Legs 1–4 biramose, rami of legs 1–3 2-segmented, those of leg 4 1-segmented. All legs without plumose setae. Leg 5 present. Egg sacs long and straight.

MALE.—No dorsal plates present. Cephalic appendages in general like those of female. Legs 1–4 biramose, all rami 2-segmented bearing plumose setae. Fifth and sixth legs present. Leg 3 endopod unmodified. Abdomen 2-segmented. Caudal rami held at distal end of abdomen. Adhesion pad with first antenna.

DISCUSSION.—A great deal of confusion has existed over the synonymy of this genus. The genus was first described by Milne-Edwards in 1840 as *Phyllophora* with *P. cornutus* as the type-species. Later, in 1861, Steenstrup and Lutken described the male as *Nogagus grandis*. Norman (1903) cited the fact that *Phyllophora* is thrice preoccupied and changed the generic name to *Phyllothereus*. Wilson (1907) discussed the preoccupation of the name *Phyllophora* and stated that Poche in 1902 suggested changing the name to *Laminifera*. This reference to Poche (1902) is in error since there is no reference to the name *Laminifera* by this author in 1902 or in subsequent works (see Brian, 1946). Brian synonymized his *Laminifera doello-juradoi* with *P. cornutus* in 1946; consequently, the valid name of the genus should be *Phyllothereus* as proposed by Norman in 1903. Wilson in 1932 states that his *Parapandarus* is so close to *Phyllothereus* that the 2 may be identical. I have examined Wilson's types of *Parapandarus* and have concluded that they are indeed the same; consequently, *P. nodosus* Wilson 1924 is synonymous with *Phyllothereus cornutus* (Milne-Edwards, 1840).

***Phyllothereus cornutus* (Milne-Edwards, 1840)**

FIGURES 125–138

Phyllophora cornuta Milne-Edwards, 1840, p. 372.
Nogagus grandis Steenstrup and Lutken, 1861, p. 386.
Phyllophorus cornutus—Bassett-Smith, 1899, p. 465.
Phyllothereus cornutus—Norman, 1903, p. 368.—Norman and Scott, 1906, p. 212.—Scott, T., and Scott, A., 1913, p. 92.—Wilson, 1932, p. 440.—Monod and Dollfus, 1938, p. 196.—Brian, 1946, p. 142.
Parapandarus nodosus Wilson, 1924a, p. 7.
Laminifera doello-juradoi Brian, 1944, p. 193; 1946, p. 142.

SPECIMENS STUDIED.—Three collections from *Prionace glauca* in the Indian Ocean (0°58′N, 55°00′E; 0°14′N, 55°00′E; 6°37′S, 55°00′E). Five collections from *Prionace glauca* at various points in the western North Atlantic.

FEMALE.—Body form as in figure 125. Average length of North Atlantic specimens 14.6 mm (based on an average of 5 specimens). Greatest width of North Atlantic specimens 10.3 mm. Average length of Indian Ocean specimens 10.3 mm (based on 4 specimens). Greatest width of Indian Ocean specimens 5.6 mm. Dorsal thoracic plates on segments 2–4. All thoracic plates paired and often greatly inflated in preserved specimens. Genital segment (fig. 126) pear shaped, being widest in posterior third. Abdomen 1-segmented, large, and bearing a dorsal plate that does not cover it when viewed dorsally. Caudal rami as in figure 126 with 4 short spines.

Oral area without adhesion pads. First antenna 2-segmented, first segment with 22 naked spines and last segment with 12 naked spines. Second antenna (fig. 127) with long terminal claw. When second antenna is flattened against oral area, claw extends posteriorly to maxillipeds. Terminal claw bearing 2 short spines. First maxilla (fig. 128) with short stout terminal spine and group of 3 short setae on basal third. Second maxilla (fig. 129) with usual fringed claw and 2 setae at base, 1 large and fringed, other shorter and plumose at tip. Maxilliped (fig. 130) bearing terminal claw with pointed tip and opposed on penultimate segment by a ridge.

Legs 1–4 (fig. 131–134) biramous with rami of legs 1–3 2-segmented and those of leg 4 1-segmented. Spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:0	0:0	I:0	0:0	VIII	III
seg. 2	VII	III	VII	VII	VIII	IV		

Leg 5 (fig. 135) consisting of an inner lobe and single outer seta.

Egg strings long and each composed of a single strand of disclike eggs.

Color whitish yellow.

MALE.—Since the male of this copepod has been well figured and described by Monod and Dollfus (1938), only a few salient features will be mentioned here. Body form as in figure 136. Oral area as in female with the following differences: second antenna smaller, in relation to rest of oral area, than in female; maxilliped with a claw at tip but opposed by 2 adhesive areas rather than 1 as in female (see Monod and Dollfus, 1938, p. 198, fig. 5).

Legs 1–4 biramose and not as highly modified as in female. Spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:0	0:1	I:0	0:1	I:1	0:1
seg. 2	IV:3	3	IV:6	8	IV:5	6	IV:5	5

Leg 5 (fig. 137) located at beginning of distal third of genital segment and consisting of a ventral lobe bearing 1 outer plumose seta, a group of 2 plumose setae and a naked spine at distal end of lobe. Leg 6 (fig. 138) located on posterior border of genital segment near junction of abdomen and consisting of an outer plumose seta and an inner naked spine.

Discussion.—*Phyllothereus cornutus* is a parasite on the gills and gill arches of a number of species of sharks, but it is most commonly found associated with *Prionace glauca*. It is cosmopolitan in distribution and has been collected by the author in both the Indian Ocean and the North Atlantic. The Indian Ocean specimens were smaller than those collected in the North Atlantic, but a detailed examination of their appendages showed no important differences. Since the same host was involved in both cases, I have concluded that they are of the same species. More collections in intermediate areas might well yield intermediate sizes. The nature of the inflated dorsal plates seems to be a function of the preserving fluid (70 percent alcohol or 10 percent formalin) as this condition has not been observed by me in life.

Genus *Gangliopus* Gerstaecker, 1854

Gangliopus Gerstaecker, 1854, p. 189. [Type-species: *G. pyriformis*.]

Female.—Frontal plate distinctly separate. First thoracic segment fused with cephalon. Thoracic segments 2–4 free and possessing dorsal plates. Dorsal plates of segment 2 small. Plate of segment 3 extending beyond tip of plate of segment 2. Plates of segment 4 partially separated. Abdomen 1-segmented, with a dorsal plate. Abdomen or its plate visible dorsally and attached to distal end of genital segment. Caudal rami lateral to abdomen. First antenna 2-segmented. Claw of maxilliped pointed at tip. Adhesion pads of the first and second antenna absent or reduced. Pad of maxilliped well developed. Legs 1–4 biramose, rami of legs 1–3 2-segmented, those of leg 4 1-segmented. All legs without plumose setae. Leg 5 present. Egg sacs long and held straight.

Male.—No dorsal plates present. Cephalic appendages like those of female. Adhesion pad with first antenna. Legs 1–4 biramose, all rami 2-segmented and bearing plumose setae. Fifth and sixth legs present. Leg 3 endopod unmodified. Caudal rami held at distal end of abdomen.

Gangliopus pyriformis Gerstaecker, 1854

FIGURES 139–146

Gangliopus pyriformis Gerstaecker, 1854, p. 192.—Wilson, 1907, p. 350.—Monod and Dollfus, 1938, p. 204.
Nogagus angustulus Gerstaecker, 1854, p. 193.
Gangliopus tetrapturi Yamaguti and Yamasu, 1960, p. 142.

SPECIMENS STUDIED.—Three collections from *Prionace glauca* in the Indian Ocean (0°58′N, 55°00′E; 0°14′N, 55°00′E; 6°37′S, 55°00′E). One collection from the same host in the North Atlantic (39°32′N, 28°02′W).

FEMALE.—Body form as in figure 139. Total length 9.1 mm (based on an average of 3 specimens). Greatest width 4.9 mm (measured at widest part of the cephalon). Dorsal thoracic plates on segments 2–4. Plates of segment 2 small and not extending to tip of plates of segment 3. Plates of segments 3 and 4 each with a deep median incision. Genital segment nearly square. Abdomen 1-segmented and joining genital segment at posterior border. Abdomen with a small dorsal plate. Caudal rami small and held at lateral angles of abdomen.

Oral area of usual pandarid type. No adhesion pad with first antenna. Adhesion pad of second antenna small and inconspicuous. Adhesion pad of maxilliped large and L-shaped (fig. 140).

Monod and Dollfus (1938) have given a detailed description of female appendages.

Legs 1–4 biramose with spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:0	0:0	I:0	0:0	VII	II
seg. 2	VII	III	X	VI	VIII	III		

Leg 5 (fig. 141) consisting of a single finger-like spine with 2 short setae. Fifth leg near junction of abdomen and genital segment.

Egg strings long and each composed of a single strand.

Color in life pale yellow and without pigment.

MALE.—Body form as in figure 142. Total length 7.4 mm (based on 1 specimen). Greatest width 3.5 mm (measured at widest part of cephalon). Thoracic segments without dorsal plates except for a winglike expansion on the posterolateral corners of segment 2. These extend nearly to end of segment 3. Genital segment (fig. 143) nearly square, 1.75 mm long by 1.85 mm wide. Genital segment with each posterior corner produced into broad lobe. Abdomen 2-segmented. Caudal rami prominent, with 4 long plumose setae and 2 smaller ones at each distal corner.

Oral area as in female except a small adhesion pad associated with first antenna. Adhesion pad of maxilliped small and incon-

spicuous. Cephalic appendages like those of female except for maxilliped (fig. 144).

Legs 1–4 biramose and with spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:1	0:1	I:1	0:1	I:1	0:1
seg. 2	IV:3	3	IV:6	8	IV:5	6	IV:5	5

Leg 5 (fig. 145) located on midlateral edges of genital segment and consisting of 3 plumose setae and 1 short stout spine. Leg 6 (fig. 146) located near junction of abdomen and genital segment and composed of a single plumose seta and a short spine.

REMARKS.—*Gangliopus pyriformis* is apparently cosmopolitan in distribution and occurs commonly on the gills of the blue shark, *Prionace glauca*. In 1960 Yamaguti and Yamasu described a new species *Gangliopus tetrapteri*. Since they do not refer to the work of Monod and Dollfus (1938), it is assumed that they were not aware of it. They based their new species on morphological differences which do not exist. Gerstaecker originally described the female as having a 2-segmented abdomen. His original description was very superficial. Monod and Dollfus (1938) updated the work and provided a working description. *Gangliopus tetrapteri* does not differ from this later description nor from my own collections in the Indian Ocean. The male was described under the name *Nogagus angustulus* by Gerstaecker at the same time as the female. No description of the male has appeared since then. I have added salient features to this original description.

Genus *Pseudopandarus* Kirtesinghe, 1950

Pseudopandarus Kirtesinghe, 1950, p. 84. [Type-species: *P. gracilis*.]
Pandarus.—Gnanamuthu, 1951a, p. 1245. [Refers to *P. longus* only.]

FEMALE.—Frontal plate distinctly separate. First thoracic segment fused with cephalon. Thoracic segments 2–4 free and possessing dorsal plates. Dorsal plates of segment 2 small and widely separated. Plate of segment 3 extending beyond tip of plates of segment 2. Abdomen incompletely divided into 2 segments and with a dorsal plate. Abdomen completely or partially concealed beneath genital segment. Abdomen attached to genital segment ventrally. Caudal rami attached terminally to abdomen. First antenna 2-segmented. Claw of maxilliped with a spatulate tip. Adhesion pads present on cephalon. Legs 1–4 biramose. Rami of legs 1–3 2-segmented, those of leg 4 1-segmented. Leg 5 present and consisting of a free segment. Egg sacs long and straight.

MALE.—I had no material of the male of this genus to study but

the male has been described by Gnanamuthu (1951) and my diagnosis is based on this description.

Body form of typical pandarid configuration. Cephalic appendages like those of female except setae on first antenna are more plumose in male. Legs 1–4 biramose with each ramus composed of 2 segments. All setae plumose. Legs 5 and 6 present. Abdomen 2-segmented. Caudal rami attached distally.

Remarks.—This genus is known only from the Indo-Pacific area and consists of 2 species from the body surface of sharks of the genera *Carcharinus* and *Triakis*. This genus may well be restricted to inshore sharks.

Key to Females of Genus *Pseudopandarus*

Abdomen concealed in dorsal view, genital segment with posterior corners produced into long pointed processes . . . . . **gracilis**
Abdomen partially visible in dorsal view, genital segment with posterior corners rounded and not greatly produced . . . . . **longus**

Pseudopandarus gracilis Kirtesinghe, 1950

Figures 147–150

Pseudopandarus gracilis Kirtesinghe, 1950, p. 84.
Pseudopandarus scyllii Yamaguti and Yamasu, 1959, p. 124.

Specimens studied.—Paratypes on loan from P. Kirtesinghe. 6 females ex *Scoliodon palasorrah*, Nosy Bé, Madagascar.

Female.—Body form as in figure 147. Total length 4.8 mm (based on an average of 3 specimens). Greatest width 1.75 mm (measured at widest part of the cephalon). Thoracic segments 2–4 with dorsal plates. Plates of segments 2 and 3 fused basally. Plates of segment 2 small and entirely lateral to those of segment 3. Plates of segment 4 covering proximal part of genital segment and fused basally. Posterior edges of plates of segments 3 and 4 often irregular in shape (I noticed this in both samples from Ceylon and Madagascar) Genital segment long (3 mm) and posterior border produced to form 2 lateral projections and median finger-like process. Abdomen (fig. 148) joined ventrally to genital segment and concealed in dorsal view. Abdomen indistinctly divided into 2 segments. A small dorsal plate present on first segment of abdomen and not extending beyond distal tip of second segment. Caudal ramus triangular in shape, widest at distal end, bearing 3 terminal naked spines and outer plumose seta. Two naked subterminal spines located at distal corners (see fig. 148).

Since this species has been well described by Kirtesinghe (1950) and Yamaguti and Yamasu (1959), only a few taxonomically important features of the appendages will be discussed here.

Oral area with prominent adhesion pads with first and second antenna. Adhesion pad of maxilliped small. Second maxilla (fig. 149) with shortest spine feathered at tip. Maxilliped (fig. 150) spatulate at tip.

Legs 1–4 biramose and with spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:0	0:0	I:0	0:0	V:3	2
seg. 2	VI	3	IV:5	7	IV:4	3		

Surface of segments of legs 1–4 generously covered with patches of spinules. Leg 5 (see fig. 148) consisting of a free segment bearing 4 naked setae (in one specimen the 2 innermost setae were fused to form a thick spine).

Egg strings long and straight.

Color in preserved specimens cream white with no pigmentation.

MALE.—Unknown.

REMARKS.—*Pseudopandarus gracilis* was described in 1950 by P. Kirtesinghe and was not reported again until 1959 by Yamaguti and Yamasu. They determined their species to be new, based primarily on the structure of the tip of the maxilliped. Unfortunately, Kirtesinghe's figure of this was misleading. I was fortunate to be able to examine type material of *P. gracilis*, in which I found that there actually were no differences between the two species on this or any other basis and thus have placed *P. scyllii* in synonymy. Yamaguti and Yamasu define the fourth leg as having 2-segmented rami. Their figure shows no articulation between segments. I have interpreted the rami as being 1-segmented. They also refer to the plate of the fourth segment as the structure that I have called the genital segment. The plate of segment 4 actually covers the proximal portion of the genital segment and is the same plate referred to by them as the plate of segment 3. The plates of segments 2 and 3 referred to as one plate belong to segment 2. A careful study of the copepod shows this interpretation to be in error and not consistent with the usual pandarid situation.

To date, this parasite has been found in the Indo-Pacific area only (Madagascar, Ceylon, Japan), parasitic on the body surface of small inshore sharks (*Carcharinus* and *Triakis*).

Pseudopandarus longus (Gnanamuthu, 1951)

FIGURES 151–161

Pandarus longus Gnanamuthu, 1951a, p. 1245.—Kurian, 1955, p. 114.

SPECIMENS STUDIED.—Four females ex *Carcharinus obesus*, 2 females ex *Rhizoprionodon acutus*, both sharks caught off Durban, South Africa.

FEMALE.—Body form as in figure 151. Total length 4.3 mm (based on 1 specimen). Greatest width 1.5 mm. Thoracic plates on segments 2–4. Plates of segment 2 small and extending only to about middle of plates of segment 3. Plate of segment 4 covering proximal end of genital segment. Genital segment long (2.6 mm), over one-half the length of body. Posterior border of genital segment with a broad midian sinus. Abdomen (fig. 152) joined ventrally to genital segment and partially concealed dorsally. Abdomen consisting of 2 incompletely separated segments. Caudal rami held at distal end of abdomen and bearing 4 terminal setae and 2 subterminal setae on outer corners. Outer terminal seta finely plumose.

Oral area with prominent adhesion pads associated with first and second antennae. Adhesion pad of maxilliped evident but somewhat reduced. First antenna (fig. 153) 2-segmented and of typical pandarid type. First segment with 24 spines, most of which are plumose. Last segment with 13 naked setae. Second antenna (fig. 154) with small claw at tip and a large adhesion pad. Mouth tube, mandible, and first maxilla of usual type. Second maxilla (fig. 155) with usual 3 spines at or near tip. Maxilliped (fig. 156) of usual type and with broad spatulate tip on last segment.

Abdomen composed of 2 segments. Caudal rami attached distally.

REMARKS.—This copepod was first described by Gnanamuthu in 1951 and assigned to the genus *Pandarus*. On the basis of the diagnostic features of the genus *Pandarus* I have removed this species and placed it in the genus *Pseudopandarus* Kirtesinghe, 1950. A comparison of *P. gracilis* Kirtesinghe and *P. longus* (Gnanamuthu) shows the following common features: the arrangement of the dorsal thoracic plates, the spatulate process of the maxilliped, the prominent first and second antennal adhesion pads with a reduction of the maxilliped pad, the nature of the abdomen and its position in relation to the genital segment, and the free segment of leg 5.

This species, like *P. gracilis*, seems to be Indo-Pacific in distribution (Ceylon and Durban, South Africa). So far, it has been reported only from carcharinid sharks.

Pannosus, new genus

Type-species: *Gangliopus japonicus* (Shiino, 1960).

FEMALE.—Frontal plate distinctly separate. First thoracic segment fused with cephalon. Thoracic segments 2–4 free and possessing dorsal plates. Dorsal plate of segment 3 extending well beyond plates of segment 2. Plates of segment 4 extends well beyond end of plate of segment 3. Plates of segments 3 and 4 fused basally. Abdomen 1-segmented. Caudal rami held laterally on abdomen. Adhesion pads of cephalon well developed. First antenna 2-seg-

mented. Claw of maxilliped spatulate. Legs 1–4 biramose, rami of legs 1–3 2-segmented, those of leg 4 1-segmented. Egg sacs long and straight.

MALE.—Unknown.

REMARKS.—This copepod was described by Shiino in 1960 from a single ovigerous female taken off a hammerhead shark (*Sphyrna zygaenae*) by him. He assigned this new species to the genus *Gangliopus*. After a redescription of the generic diagnosis of this genus, it became apparent that this new copepod did not belong to that genus. Since I have had no material of this species to work with, no further diagnosis of Shiino's species can be made. I have removed this species from the genus *Gangliopus* for the following reasons: (1) Shiino's species show well-developed adhesion pads associated with the first and second antennae; (2) the dorsal thoracic plates of the second segment are well formed in *Pannosus;* (3) the maxilliped of *japonicus* has a spatulate tip whereas in *Gangliopus* the tip is pointed. Shiino does not mention the presence of fifth legs but more material would probably reveal their nature.

Since this copepod does not conform to any known genus, I propose placing it in a new genus *Pannosus*.

The name *Pannosus*, from Latin, meaning "covered with rags," refers to the appearance of the dorsal plates.

Genus *Perissopus* Steenstrup and Lütken, 1861

Perissopus Steenstrup and Lütken, 1861, p. 393. [Type-species: *P. dentatus*.]
Chlamys Beneden, 1892a, p. 227.
Achtheinus Wilson, 1908, p. 450.

FEMALE.—Frontal plate not distinctly separate. First thoracic segment fused with cephalon. Thoracic segments 2–4 free and possessing dorsal plates. Dorsal plate of segment 2 extending to posterior border of plates of segment 3. Plates of segment 4 covering anterior portion of genital segment. Abdomen 1-segmented and attached ventrally to genital segment. Caudal rami rudimentary. First antenna 2-segmented. Second antenna armed with teeth at tip. Mouth parts of typical pandarid type. Adhesion pads present. Maxilliped with small claw and large adhesion pad. Legs 1–4 biramose but much reduced. Rami of legs 1 and 2 2-segmented. Rami of legs 3 and 4 1-segmented. All legs without plumose setae. Legs 5 and 6 present. Egg strings long and straight.

MALE.—Frontal plate separate. No dorsal plates present. Oral area similar to female but with adhesion pads reduced. Maxilliped with a strong terminal claw. Legs 1–4 biramose with each ramus 2-segmented. All setae plumose. Fifth and sixth legs present. Leg 3

endopod unmodified. Abdomen 2-segmented. Caudal rami attached distally to abdomen.

DISCUSSION.—This genus is represented by two species, *Perissopus dentatus* Steenstrup and Lütken 1861 and *P. oblongatus* (Wilson, 1908). A discussion of the history of the synonomy of these species is included in the species descriptions.

Perissopus oblongatus (Wilson, 1908)

Achtheinus oblongatus Wilson, 1908, p. 450.
Achtheinus dentatus Wilson, 1911, p. 630.
Achtheinus pinguis Wilson, 1912, p. 235.
Achtheinus japonicus Wilson, 1922, p. 4.
Achtheinus parvideus Wilson, 1923, p. 7.
Achtheinus intermedius Kurtz, 1924, p. 614.
Achtheinus galeorhini Yamaguti, 1936, p. 11.
Achtheinus platensis Thomsen, 1949, p. 20.
Achtheinus chinesis Thomsen, 1949, p. 23.
Achtheinus impenderus Shen and Wang, 1958, p. 27.

DISCUSSION.—In 1908 Wilson described a new copepod and erected for it a new genus, *Achtheinus*. Since then, 10 species assigned to this genus have been described. A comparison of the description and figures of these species show that they should be included in the genus *Perissopus*. This is apparent when one compares the appendages of the two groups. In both, the second antenna has a hoodlike process bearing spines. The maxillipeds of each bears a reduced claw and the basal segment is in the form of a flattened pad. Legs 1–4 are much reduced in both and are similar in form.

I have grouped all species described in the genus *Achtheinus* as one species. These had been separated on the basis of overall form and not on details of the appendages. It is apparent that we have here a situation like that found in *Perissopus dentatus*—a single species with variation in body form. I have examined Wilson's material of *A. oblongatus*, *A. dentatus*, and *A. pinguis*, and I could find no good basis for keeping them as separate species. On the basis of the descriptions of other species, there is no valid evidence to justify more than one species. Probably the best description of the appendages of this species can be found in Yamaguti's (1936) description of *A. galeorhini*.

This species can be separated from *P. dentatus* on the basis of 2 characters. In *P. dentatus* the posterior corners of the genital segment are sharply angular whereas in *P. oblongatus* they are rounded. In *P. dentatus* the endopods of legs 1–4 are unarmed. In *P. oblongatus* the endopods of legs 1 and 2 and sometimes 3 are armed with short setae.

I did not collect this copepod and more material would certainly

be desirable to clarify this situation. It may be that future descriptions will warrant resurrecting some of the previously described species but, on the basis of existing descriptions, this is not justified.

So far, this species has been reported from a number of inshore species of sharks, especially of the genera *Triakis* and *Acanthias*. It is a parasite on the body surface of its host.

Perissopus dentatus Steenstrup and Lütken, 1861

FIGURES 162–189

Perissopus dentatus Steenstrup and Lütken, 1861, p. 393.—Richiardi, 1880, p. 148.
Perissopus communis Rathbun, 1887, p. 560.
Chlamys incisus Beneden, 1892a, p. 227.
Perissopus crenatus Leigh-Sharpe, 1930, p. 7.
Perissopus manuelensis Gnanamuthu, 1951a, p. 1252.
Perissopus travancosiensis Kurian, 1955, p. 108.
Perissopus serratus Heegaard, 1962, p. 175.

SPECIMEN STUDIED.—Five females and 1 male ex *Carcharinus milberti* from Sarasota, Fla., 1 female ex *C. leucas*, Sarasota, Fla., 4 females ex *C. maculipinnis*, Sarasota, Fla., and 3 females ex "shark" from Siboga Expedition, 2 females ex *Mustelus* species Durban, South Africa.

All descriptions and figures refer to specimens from *Carcharinus milberti* unless otherwise stated.

FEMALE.—Body form as in figures 162, 187, 188, and 189. Total length 4.9 mm (based on 1 specimen). Greatest width 3.8 mm (measured at widest part of cephalon). Frontal plate not completely separated from cephalon. First thoracic segment fused with cephalon. Thoracic segments 2–4 free and with dorsal plates. Plates of segment 2 widely separated and extending only to distal tip of plates of segment 3. Plates of segment 4 extending only slightly over proximal portion of genital segment. Genital segment large, comprising about one-half total body length. Shape of genital segment variable (see figs. 162, 187, 188, 189). Abdomen (fig. 163) 1-segmented, nearly hidden in dorsal view. No dorsal plate evident. Caudal rami joined distally to abdomen, articulated on dorsal surface only. Each ramus with 7 short spines along posterior border.

Oral area of usual pandarid type. Adhesion pads moderately developed and associated with first and second antenna and maxilliped. No pad on outer distal corners of cephalon. First antenna (fig. 164) 2-segmented. First segment with 18 spines, armed as in figure. Second segment with 11 naked setae. Second antenna (fig. 165) with small adhesion pad at base, last segment in form of claw with very small spine near base. Tip of claw (fig. 166) with curious hooded appearance. Mouth tube of usual type, labium fringed at tip (fig.

167). Mandible of usual form. First maxilla (fig. 168) consisting of broad basal lobe with short spine at tip and group of 3 short setae. Second maxilla with tip armed as in figure 169. Maxilliped (fig. 170) large. Terminal spine small but opposed by a very broad adhesion area. Surface of adhesion area shows imprint of host denticles suggesting a secretion of a cement-like substance on surface of the maxilliped. The maxilliped can be easily pulled off the copepod when removing the parasite from the host.

Legs 1–4 (figs. 171–174) biramose. Spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:0	0:0	IV	0	IV	0
seg. 2	IV	0	IV	0				

Legs 1–4 small and weakly developed. Endopod of all legs unarmed except for patches of spinules. Segmentation reduced in legs 3 and 4. Leg 5 (fig. 175) consisting of a single lobe with 4 naked setae, situated near the ventral distal corner of genital segment (see fig. 163). Leg 6 (fig. 176) consisting of 2 unarmed lobes located near junction of abdomen and genital segment (see fig. 163).

Egg strings long and straight.

Color in life cream white without pigmentation.

Male.—Body form as in figure 177. Total length 2.9 mm (based on 1 specimen). Greatest width 1.4 mm (measured at widest point of cephalon). Cephalon rounded. Frontal plate distinctly separate. Thoracic segments 2–4 free. No dorsal plates present. Genital segment longer than wide with posterior corners rounded and scarcely projecting posteriorly. Spermatophores visible within. Abdomen 2-segmented. Caudal ramus (fig. 178) about as long as wide with 4 long terminal plumose setae and 2 short subterminal ones on distal corners of each ramus. Four terminal setae all nearly equal in length.

Oral area similar to that of female. Adhesion pads reduced. First antenna as in female. Second antenna as in figure 179. Oral appendages as in female. Maxilliped (fig. 180) with a strong terminal claw opposed by an area of heavy ridges on basal segment.

Legs 1–4 biramose. Spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:1	0:1	I:1	0:1	I:1	0:1
seg. 2	III:4	3	III:6	8	II:6	6	III:5	4

Leg 1 (fig. 181) with each ramus 2-segmented but exopod only weakly divided into 2 segments. Legs 2–4 (figs. 182–184) with each ramus strongly divided into 2 segments. All setae plumose. Leg 5 (fig.

185) located on midlateral edge of genital segment and consisting of a group of 3 setae and 1 stout spine. All setae naked, spine finely barbed. Leg 6 (fig. 186) located near junction of abdomen and genital segment and consisting of a single naked seta and a finely barbed stout spine.

Color in life cream white, no pigment.

Remarks.—To date, 7 species of *Perissopus* have been described. I have examined material of this genus from several hosts and noted wide variation in body form. A closer examination of the appendages showed no differences between one form and another. Unfortunately, I had only a few specimens of each type available. Figure 187 shows an adult female from *Carcharinus leucas*, Sarasota, Fla. Its measurements are 4.4 by 2.2 mm. Figure 188 is an adult female from *Carcharinus maculipinnis*, Sarasota, Fla. (3.9 by 2.4 mm). Figure 189 is an adult female from the Siboga Expedition to the Indo-Pacific, host recorded only as a "shark." It measures 3.8 by 2.2 mm. A cursory examination of these would indicate more than one species, but I must, on the basis of the few specimens available, concur with Capart (1953), who noticed this same variation and concluded that they should be treated as 1 species.

More material from these and other hosts may favor splitting the genus into a number of species but, in the face of so small a sample, I do not feel justified in doing this at the moment. One would expect to find at least minor differences in the finer details if they are indeed separate species. None seem to exist. I have thus placed all known species in synonymy as *Perissopus dentatus*. Apparently Heegaard (1962) did not know of the new species of Gnanamuthu or Kurian when he described *Perissopus serratus*.

Perissopus dentatus seems to be a parasite of inshore species of sharks. The copepod is often found externally attached near the nares and less often near the posterior border of the fins. It is the only pandarid that attaches to its host by the use of cement. As pointed out above, the maxilliped of the female bears a very large pad that, upon removal of the copepod from the host, often shows denticles or the impression of denticles adhering to the surface of this pad. This adaption may be due to the rather hazardous area of attachment on the host (nose). Undoubtedly the nose of the host is often bumped, thus requiring an effective hold-fast structure if the parasite is to remain on the host.

The male is described here for the first time. It was attached to a female when found.

Genus *Dinemoura* Latreille, 1829

Caligus Müller, 1785, p. 132. [Refers to *C. productus* only.]
Dinemoura Latreille, 1829, p. 197. [Type-species: *D. producta*.]
Binoculus Nordman, 1832, p. 38.
Dinematura Burmeister, 1833, p. 284.
Pandarus.—Baird, 1850, p. 286. [Refers to *P. lamnae* only.]
Nogagus.—Milne-Edwards, 1840, p. 460. [Refers to *N. gracilis* only.]

FEMALE.—Frontal plate distinctly separate. Thoracic segments 2–4 free. Dorsal thoracic plates on segment 4. Genital segment large. Abdomen 2-segmented and joined to genital segment ventrally. Caudal rami broad. Oral area with or without adhesion pads. Adhesion pad of first antenna double when present. Second maxilla with a patch of long setules at base of terminal claw. Maxilliped with small terminal claw. Legs 1–4 biramose. Rami of leg 1 2-segmented. Rami of legs 2 and 3 3-segmented. Rami of leg 4 1-segmented and in form of broad lamellae. Egg strings long and straight or folded.

MALE.—Body form of usual pandarid type. Dorsal plate of segment 4 reduced. Abdomen 2-segmented. Caudal rami large. Oral area as in female. Legs 1–4 biramose. Legs as in female with the following exceptions: terminal segment of endopod of leg 3 modified; leg 4 rami 2-segmented; legs 5 and 6 present.

DISCUSSION.—The genus *Dinemoura* occurs on the body surface of large pelagic sharks. The genus is represented by 4 valid species.

There has been much confusion in the literature over the generic name of this group. In 1829 Latreille separated *Caligus productus* Müller from the genus *Caligus* and assigned it to a new genus, *Dinemoura*. In 1832 Nordman used the name *Binoculus* but this was preoccupied by Geoffroy in 1792 for a phyllopod genus. Burmeister changed the name *Dinemoura* to *Dinematura* in 1833 because the etymology of the word *Dinemoura* was incorrect. Since then, the 2 names have appeared with almost equal frequency. Yamaguti (1963) suggested that the original name be the proper one. According to Article 33a of the "International Code of Zoological Nomenclature," this viewpoint is correct. Burmeister's change was an "unjustified emendation" and cannot stand. Not enough is known of the males of the 4 species on which to base a key, but one is provided below for the females.

Key to Females of Genus *Dinemoura*

1. Adhesion pads conspicuous on oral area 2
   Adhesion pads absent or reduced on oral area 3
2. Genital segment about ½ body length. Dorsal plates of segment 4 wider than long . . . . . **latifolia**
   Genital segment about ⅔ body length. Dorsal plates of segment 4 longer than wide . . . . . **producta**

3. Posterior corners of genital segment not greatly produced and rounded. **ferox**
Posterior corners of genital segment greatly produced and truncated. **discrepans**

Dinemoura producta (Müller, 1785)

FIGURES 190, 191

Caligus productus Müller, 1785, p. 132.
Dinemoura producta.—Latreille, 1829, p. 197.—Krøyer, 1837, p. 202.—Scott, T., 1901, p. 124.—Scott, T., and Scott, A., 1913, p. 86.—Norman and Scott, T., 1906, p. 211.—Norman and Brady, 1910, p. 404.—Fage, 1923, p. 281.—Pesta, 1934. p. 27.—Oorde and Schuurmans Stekhoven, 1936, p. 139.—Matthews and Parker, 1950, p. 568.—Barnard, 1955, p. 262.—Delamare-Debouteville and Nunes-Ruivo, 1958, p. 223.
Binoculus productus.—Nordman, 1832, p. 38.
Dinematura gracilis Burmeister, 1833, p. 284.
Dinematura producta.—Burmeister, 1833, p. 331.—Steenstrup and Lütken, 1861, p. 370.—Norman, 1868, p. 301.—Bassett-Smith, 1899, p. 463.—Scott, T., 1900, p. 156.—Brian, 1906, p. 52; 1911, p. 197; 1944, p. 202.—Wilson, 1907, p. 380; 1923, p. 8; 1932, p. 431.—Hansen, 1923, p. 35.—Scott, A., 1929, p. 95—Pesta, 1934, p. 27.—Heegaard, 1943b, p. 26; 1945, p. 15.—Delamare-Debouteville, 1948, p. 446.—Matthews and Parker, 1950, p. 568.—Rose and Vaissiére, 1953, p. 86.—Yamaguti, 1963, p. 117.
Pandarus lamnae Johnston, 1835, p. 203.
Nogagus gracilis.—Milne-Edwards, 1840, p. 460.
Dinemoura lamnae Baird, 1850, p. 286.
Nogagus productus.—Gerstaecker, 1853, p. 63.
Dinematura lamnae.—Krøyer, 1863, p. 179.
Dinematura affinis Thomsen, 1949, p. 14.—Shiino, 1957, p. 365.

SPECIMENS STUDIED.—Single collections from each of the following hosts: *Isurus oxyrhynchus* Rafinesque (35 00′N, 70 00′W), *Prionace glauca* (Linnaeus) (39 32′N, 28 02′W), *Carcharodon carcharias* (Linnaeus) off Boothbay Harbor, Maine, *Cetorhinus maximus* (Gunnerus) on loan from Zoological Museum in Amsterdam.

FEMALE.—A good description of the female of this species has been given as recently as 1957 by Shiino. His description is of *Dinematura affinis* but, since this is synonymous with *Dinemoura producta*, the figures and description apply. I will therefore only point out salient features.

Body form as in figure 190. Total length (based on an average of 2 specimens) 18.5 mm. Greatest width 8.0 mm. Dorsal thoracic plates, present only on segment 4 fused basally and covering the anterior third of the genital segment. Genital segment about ⅔ body length. Caudal rami broad and with setae placed laterally. (Wilson, 1907, showed them as terminal, but in all specimens I examined they are laterally displaced.) Oral area as in figure 191. First antenna 2-segmented and bearing stout spinose spines on first segment and short naked setae on terminus of last segment. Second antenna with a stout claw, sharply bent at tip. Mandible of usual type with 12

teeth on tip and projecting within mouth tube as in other members of group. First maxilla of 2 segments with a palplike process bearing 3 short setae on first segment. Second maxilla with usual fringe claw at tip, a stout subterminal spine and a subterminal patch of long hairs. Maxilliped with a short claw at tip.

Legs 1–4 biramose. Rami of leg 1 2-segmented. Rami of legs 2 and 3 3-segmented. Rami of leg 4 1-segmented and modified to form broad lamellae. Spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:1	0:1	I:1	0:1	V	0
seg. 2	IV:3	3	I:1	0:2	I:1	0:2		
seg. 3	–	–	III:5	6	III:5	4		

Leg 5 consisting of a small process bearing 2 short spines, outer plumose the inner naked. Leg 5 located near junction of abdomen and genital segment.

Egg strings long and straight.

Color in life cream, generally devoid of pigment.

Male.—The male of this species was first described by Wilson (1923). Because I had no material of the male of this genus, I am unable to expand Wilson's work. He failed to mention any modification of the endopod of leg 3. Based on evidence in other members of the genus, this modification should be present. On the basis of Wilson's work the male appendages appear to be very similar to those of the female, except that the fourth leg of the male is not modified into broad lamellae as in the female but rather each ramus is 2-segmented and bears spines and setae.

Remarks.—This copepod has a very long and confusing history. It has been described or recorded under 11 different names. Many of the synonyms have been noted in the literature previously (mainly Wilson, 1907) but I have, in addition to these, placed *D. affinis*, Thomsen, 1949, in synonymy with *D. producta*. Shiino (1957) described and illustrated *D. affinis* from Japan. These descriptions agree with material I have collected and identified as *D. producta* from the Atlantic from 4 different hosts, including the same host from which Thomsen described *D. affinis*. In view of this, I feel certain that only one species of copepod is involved here.

D. producta is found on several species of pelagic sharks but is most commonly associated with sharks of the genera *Lamna* and *Isurus*. It is probably worldwide in distribution.

Dinemoura ferox (Krøyer, 1838)

FIGURES 192, 193

Dinematura ferox Krøyer, 1838, p. 40.—Steenstrup and Lütken, 1861, p. 376.—Olsson, 1868, p. 17.—Meirs, 1880, p. 71.—Bassett-Smith, 1899, p. 463.—Wilson, 1907, p. 377; 1920, p. 7.—Hansen, 1923, p. 33.—Stephensen, 1940, p. 5.—Yamaguti, 1963, p. 117.
Dinemoura ferox.—Milne-Edwards, 1840, p. 465.
Dinemoura elongatus Beneden, 1857, p. 226.
Dinematura carcharodonti Thomson, 1889, p. 360.

SPECIMENS STUDIED.—Two collections from the U.S. National Museum: USNM 12036 from a shark caught off Iceland, USNM 37783 (no collection data).

FEMALE.—Body form as in figure 192. Total length 32 mm (based on 1 specimen). Greatest width 10 mm. The female of this species has been well illustrated by Krøyer (1838) and Steenstrup and Lütken (1861) so that I will not repeat the figures here. Dorsal thoracic plates on segment 4. Plates extending slightly over proximal portion of genital segment. Genital segment large, about one-half body length. Abdomen 2-segmented. First segment bearing lateral wing-like projections. Caudal rami large and with 4 short spines along distal margin. Oral area as in figure 193. No adhesion pads associated with first and second antenna. A small pad with maxilliped. Oral appendages as in *D. producta*. The claw of the maxilliped is larger in *D. ferox* than in *D. producta*.

Legs 1–4 as in figure 193. Spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:1	0:1	I:1	0:1	IV	IV
seg. 2	IV:3	3	I:1	0:2	I:1	0:2		
seg. 3			III:5	6	III:5	4		

Legs 5 and 6 represented by a series of lobes on posterior ventral surface of genital segment (see fig. 193). Lobes nearest to attachment of abdomen probably represent leg 6. Single most posterior lobe undoubtedly represents leg 5.

Egg strings long and straight.

Color in preserved specimens cream yellow and lacking pigment.

MALE.—Hansen (1932) described a copepod identified by Krøyer as the male of *D. ferox*. He did not mention the presence of spermatophores which should be the foremost character relating to its sex. The fourth legs are not modified as in the female. The description in general is insufficient; that this is actually the male of *D. ferox*

is inconclusive. It appears to be of the genus, however. Consequently, the male of this species still remains poorly known and perhaps even yet to be described.

Discussion.—*Dinemoura ferox* is the largest pandarid copepod yet described. It is almost twice as long as its next largest relative. This alone easily separates it from other members of the group. It has been reported only from sharks from the North Atlantic in the area of Greenland. The known hosts are *Somniosus microcephalus* (Bloch and Schneider), reported by Wilson (1920), and *Centrophorus squamosus* Müller and Henle, reported by Hansen (1923). Miers (1880) reported this copepod taken off the "Greenland shark" and noted that the copepods were usually but not always found attached to the eyes of the host.

Dinemoura latifolia (Steenstrup and Lutken, 1861)

Figures 194–196

Dinematura latifolia Steenstrup and Lütken, 1861, p. 378.—Heller, 1868, p. 199.—Richiardi, 1880, p. 148.—Valle, 1880, p. 60.—Carus, 1884, p. 390.—Brian, 1898b, p. 14; 1899, p. 4; 1902, p. 17; 1906, p. 52; 1944, p. 201.—Bassett-Smith, 1899, p. 463.—Wilson, 1907, p. 383; 1923, p. 15; 1932, p. 432; 1935b, p. 778.—Yamaguti, 1936, p. 9; 1963, p. 117.—Shiino, 1954, p. 318; 1957, p. 365.—Delamare-Deboutteville and Nunes-Ruivo, 1954, p. 204.—Barnard, 1955, p. 263.—Heegaard, 1962, p. 177.

Specimen studied.—Two collections from *Isurus oxyrinchus* Rafinesque in the North Atlantic (42°18′N, 64°02′W; 35°00′N, 70°00′W). A single collection from the same host in the Indian Ocean (8°55′S, 55°08′E).

Female.—Body form as in figure 194. Total length 14.5 mm (based on an average of 5 specimens). Greatest width 8.2 mm. Dorsal thoracic plates on segment 4 projecting posteriorly over the anterior portion of genital segment. Genital segment about one-half body length. Abdomen 2-segmented, each segment with a dorsal plate. Caudal rami large, each bearing 4 setae. Oral area as in figure 195.

Since the female of this species has been well described and figured by Yamaguti (1936) and Shiino (1954), I will only discuss salient features. Adhesion pads associated with first and second antenna and maxilliped. Oral appendages similar to those of *D. producta*.

Legs 1–4 biramose with spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:1	0:1	I:1	0:0	V	0
seg. 2	IV:3	3	I:1	0:2	I:1	0:2		
seg. 3			III:5	6	III:5	4		

Shiino (1947) stated that the fifth legs are still undiscovered. I have

figured the posteroventral surface of the genital segment (fig. 196). This region shows 2 areas representing legs 5 and 6. I have interpreted the single, broad, spatulate process as belonging to leg 5 and the curved, clawlike process at the junction of the genital segment and abdomen as leg 6.

MALE.—The male of this species has been described with some figures by Wilson (1907). Because I had no material of the male of this species, I am unable to amplify this description. Wilson did show some modification on the endopod of leg 3 (Wilson, 1907, p. xxv, fig. 103) which supports my contention that this is characteristic of the males of the entire group II of the family. The figures and description are incomplete and more material would certainly be desirable to complete the male description of this species. He stated that the fourth legs are not laminate as in the female but each ramus is 2-jointed and bearing spines and setae. He did not figure this appendage.

DISCUSSION.—This is a fairly common species occurring on the body surface of a number of pelagic sharks of the genera *Isurus*, *Lamna*, and *Carcharodon*. These 3 genera of sharks compose the family *Isuridae* (after Bigelow and Schroeder, 1948). The parasite may well be restricted to that group. It is easily separated from members of the genus by the shape of the dorsal thoracic plates.

Dinemoura discrepans, new species

FIGURES 197–217

SPECIMENS STUDIED.—Eighteen females and 13 males from the body surface of *Alopias vulpinus* (Bonneterre) from the Indian Ocean (9°24′N, 54°58′E). Holotype female (USNM 113592), allotype male, and 10 paratypes (5♀ ♀, 5♂ ♂) deposited in alcohol in the U.S. National Museum, 10 paratypes (5♀ ♀, 5♂ ♂) in the British Museum (Natural History), and the remaining paratypes in the author's collection.

Other specimens studied: a single collection from *Alopias vulpinis* in the Indian Ocean (7°17′N, 55°00′E); a single collection from *Alopias superciliosus* (Lowe) from Nosy Bé, Madagascar; a single collection from *Alopias superciliosus* from the Pacific Ocean (0°38′N, 124°23′W).

FEMALE.—Body form as in figure 197. Total length 13.9 mm (based on an average of 5 specimens). Greatest width 6.7 mm (measured at widest part of cephalon). Cephalon rounded, 6.7 mm by 6.2 mm, slightly wider than long. Thoracic segments 2–4 free. Posterior corners of segment 2 produced to form winglike expansions. Dorsal plates present on segment 4. Plate of segment 4 extending only slightly over anterior portion of genital segment with their

posterior borders serrate. Plates widely separated. Genital segment longer than wide (5.7 by 3.9 mm). Posterior corners of genital segment produced and truncated. Abdomen 2-segmented. Each segment bearing a dorsal plate. Plate of segment 1 bilobed. Plate of segment 2 single. Caudal ramus large (1.6 by 0.8 mm) and bearing 6 short, naked spines.

Oral area as in figure 198. Adhesion pads reduced. First antenna (fig. 199) 2-segmented. First segment with 29 short, stout spines (majority of the spines covered with spinules). Second segment with 14 naked setae. Second antenna (fig. 200) with a terminal claw recurved at tip, with 2 short spines along outer edge. Small adhesion areas on the penultimate segment. Mandible (fig. 201) of the usual type with 11 teeth at tip (fig. 202). First maxilla (see fig. 201) a broad lobe with a group of 3 setae near base and a broad terminal spine. Second maxilla (fig. 202) with terminal claw subdivided into 2 segments (fig. 204). Terminal segment with short rows of fringe. Penultimate segment with group of broad bladelike setae on inner distal corner and surface of segment covered with stout setules. Antepenultimate segment with large spine and patch of hairs at inner distal corner. Maxilliped (fig. 205) with strong terminal claw.

Legs 1–4 biramose. Spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:1	0:1	I:1	0:0	4	0
seg. 2	IV:3	3	I:1	0:2	IV:6	0:2		
seg. 3			III:5			4		

Leg 1 (fig. 206) with both rami 2-segmented. No adhesion pads on the rami. Leg 2 (fig. 207) with each ramus 3-segmented. Outer edge of first exopod segment striated as an adhesion area. Outer edges of other exopod segments serrated. Leg 3 (fig. 208) with exopod of only 2 clearly separated segments. Terminal segment shows some evidence of being subdivided but indicates a fusion of last 2 segments. Leg 4 with each ramus in shape of a broad lamella (see fig. 198). Exopod bearing 4 short spines. Endopod unarmed. Leg 5 (see fig. 209) a single lobe with 1 small setae. Leg 6 (see fig. 219) located near junction of abdomen and genital segment and composed of 2 spatulate processes projecting under lateral extensions of first abdominal segment. Two sclerotized areas located on the midline of genital segment. These probably function in attachment of spermatophores.

Egg strings long and folded (fig. 210) forming 3 strands.

Color in life cream and without pigmentation.

Male.—Body form as in figure 211. Total length 9.7 mm (based on an average of 2 specimens). Greatest width 5.1 mm (measured at the widest part of the cephalon). Cephalon about one-half body

length. Dorsal thoracic plates present on segment 4 and similar to those of female. Genital segment with posterior corners produced to form lobes serrate on posterior border (see fig. 212). Genital segment slightly longer than wide (2.8 by 2.3 mm). Abdomen 2-segmented and without dorsal plates. Caudal rami as in female.

Oral area as in female. Legs 1–3 as in female except for a modification on endopod of leg 3 (fig. 213). This appendage may be used in the transfer of spermatophores to female. Leg 4 (fig. 214) with rami 2-segmented and not modified in form of lamellae. Spine and setal formula of legs 1–4 as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:1	0:1	I:1	0:0	I:0	0:1
seg. 2	IV:3	3	I:1	0:2	IV:6	0:2	VI	III
seg. 3		III:5	6	6		4		

Leg 5 (fig. 215) located at the midpoint of the lateral margin and composed of an outer lobe with 2 setae (outer plumose, inner naked) and an inner lobe with a single naked setae. Leg 6 (fig. 216) near junction of abdomen and genital segment and consisting of a small process bearing a single naked spine.

Spermatophores (fig. 217) attach to female and cross to opposite seminal receptacle as in other members of the family. It is less obvious in this group since the spermatophores lie side by side in close proximity to each other. Figure 217 shows one spermatophore removed to reveal neck of the other spermatophore crossing to receptacle of other side.

Color cream white as in female and devoid of pigmentation.

Discussion.—This parasite seems to be specific to sharks of the genus *Alopias*. I have examined material from the Indian Ocean and Pacific and it may well be found throughout the range of the host genus. This species is easily separated from the known members of the genus by the shape of the genital segment and nature of the dorsal thoracic plates. It is found on the body surface of the host and, from my own experience, seems to favor the undersurface of the host in the region of the cloaca. The description of the male should give pertinent information regarding the nature of the lesser known males of other species of this genus. The modification of the endopod of leg 3 is quite distinct. It is interesting to note that the male and female are much more alike than in members of group I of this family. This may prove to be a consistent difference between these two groups.

The word *discrepans* is from Latin, meaning "to differ."

Genus *Demoleus* Heller, 1865

Caligus.—Otto, 1821, p. 15. [Refers to *C. heptatus* only.]
Binoculus.—Nordman, 1832, p. 32. [Refers to *B. sexsetaceus* only.]
Dinematura.—Burmeister, 1833, p. 331. [Refers to *D. sexsetaceus* only.]
Nogagus.—Gerstaecker, 1853, p. 63. [Refers to *N. productus* only.]
Demoleus.—Heller, 1868, p. 199. [Type-species: *D. paradoxus.*]

Female.—Frontal plate distinctly separate. Thoracic segments 2–4 free. Dorsal thoracic plates on segment 4 only. Abdomen 1-segmented and with a dorsal plate. Caudal rami large. Oral area with adhesion pads associated with first and second antenna, maxilliped and an additional pad between bases of the maxillipeds. Oral appendages of usual type. The second antenna with terminal hook-like spine reduced. Penultimate segment of second maxilla with large spine and patch of stout setules on distal corner. Legs 1–4 biramose; all rami 2-segmented. Legs 5 and 6 present. Egg strings folded.

Male.—Body form of usual type. No dorsal plates present. Oral area similar to that of female. Appendages similar to female except for a modification on endopod of third leg of male. Males of this genus are poorly known.

Discussion.—At present there are 2 species in this genus. *D. heptatus*, female, is well known and is amply recorded in the literature principally as an external parasite of *Hexanchus*. *D. latus* is reported by Shiino (1954) from *Acanthidium eglantina* (Jordan and Snyder) and I have examined material from *Squalus acutipinnis* Regan. Both of these hosts are members of the family Squalidae.

The adhesion process between bases of maxillipeds is not found in any other genus in this family. This character alone sets it apart from other pandarid copepods.

Key to Females of Genus *Demoleus*

Genital segment covering the dorsal abdominal plate. Egg strings exposed. **heptatus**
Genital segment only covering about ½ of the dorsal abdominal plate. Egg strings hidden . . . . . **latus**

Demoleus heptatus (Otto, 1821)

Figures 218–237

Caligus heptatus.—Otto, 1821, p. 15.
Caligus paradoxus Otto, 1828, p. 352.
Binoculus sexsetaceus Nordman, 1832, p. 32.
Dinematura sexsetaceus.—Burmeister, 1833, p. 331.
Nogagus productus Gerstaecker, 1853, p. 64.

Demoleus paradoxus.—Heller, 1868, p. 199.—Carus, 1884, p. 361.—Bassett-Smith, 1899, p. 460.—Pearson, 1905, p. 166.—Brian, 1906, p. 50.—Wilson, 1907, p. 349; 1935b, p. 778.—Scott, T., and Scott, A., 1913, p. 79.—Rose and Vaissiere, 1953, p. 85.

Demoleus heptatus.—Dollfus, 1943, p. 1.—Yamaguti, 1963, p. 115.

SPECIMENS STUDIED.—Eleven females and 1 male USNM 60465 from *Hexanchus* species from Monterey Bay, California.

FEMALE.—Body form as in figure 218. Total length 12.5 mm (based on a single specimen). Greatest width 4.5 mm (measured at widest part of cephalon). Carapace rounded about as long as wide. Dorsal thoracic plates present on segment 4. Plates extending only slightly over anterior portion of genital segment. Genital segment 5.8 mm long and 3.1 mm wide, about one-half body length. Posterior corners produced dorsally and extending as rounded lobes over abdomen and caudal rami. Abdomen (see fig. 219) 1-segmented and with a large dorsal plate. Caudal rami large (2.6 by 1.3 mm), joined to the abdomen distally (see fig. 219). Each ramus with 6 naked setae, innermost and outermost very short.

Oral area (fig. 220) with adhesion pads associated with first and second antenna and maxilliped. Adhesion pads small and not well developed. A padlike process located between bases of maxillipeds (fig. 221). This process is directed posteriorly and has a pad at tip. Pad is divided by a median line suggesting a fusion of 2 pads. First antenna (fig. 222) 2-segmented. First segment with 28 spines and setae armed as in figure. Last segment with 9 naked setae. Second antenna (fig. 223) small. Terminal claw not well developed. Adhesion area near base. Mouth tube of the usual form. Mandible with 12 teeth at tip. First maxilla (fig. 224) composed of a lobe with articulated process at tip and basal process bearing 3 short spines. Second maxilla of usual form. Terminal claw (fig. 225) subdivided. Distal segment with rows of fringes as in figure. Subterminal segment with patch of spines. Penultimate segment bearing prominent spinose spine and group of long hairs. Maxilliped (fig. 226) with terminal claw opposed by sclerotized protuberances on basal segment.

Legs 1–4 (figs. 227–230) biramose. Spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:1	0:1	I:1	0:1	I:1	0:1
seg. 2	IV:3	3	IV:5	8	IV:5	6	IV:5	5

Leg 5 (fig. 231) located on ventral surface of genital segment near lateral margin (see fig. 219) and composed of single lobe with 2 naked spines. Leg 6 (fig. 232) at area of spermatophore attachment and modified to assist in this function.

Egg strings folded to form 3 strands.

MALE.—Body form as in figure 233. Total length 9 mm (based on 1 specimen). Greatest width 3.4 mm. No dorsal plates present. Oral area as in female. First antenna as in female. Second antenna (fig. 234) with clawlike tip. Penultimate segment with stout hooklike spine at midpoint. Other oral appendages as in female. Maxilliped (fig. 235) with long terminal claw opposed by 4 adhesive areas on preceding segments. Legs 1–4 as in female except for modification of last segment of endopod of leg 3 (fig. 236). Leg 5 single lobe with 2 or 3 setae. In the only specimen I was able to observe one leg was broken and the other was not clear. Leg 5 located along margin of genital segment near midpoint. Leg 6 (fig. 237) located near junction of abdomen and genital segment and composed of a single lobe with 2 naked setae.

DISCUSSION.—*Demoleus heptatus* has been described and its synonymy considered recently by Dollfus (1943). The male is poorly known and has been elaborated here on the basis of a single specimen. This parasite seems to be most common on sharks of the genus *Hexanchus*.

Wilson designates *Nogagus grandis* Steenstrup and Lütken as the male. This has been shown to be the male of *Phyllothyreus cornutus* Milne-Edwards. The true male is not well known and the single specimen that I studied may be the first record of the true male of this species.

Demoleus latus Shiino, 1954

FIGURES 238–242

Demoleus latus Shiino, 1954, p. 325.

SPECIMENS STUDIED.—A single collection of 12 females from the *Discovery* Collections, collected off Cape Trawler, July 8, 1927, from *Squalus acutipinnis*.

FEMALE.—This species has been well described and figured by Shiino (1954). Except for the inclusion of a few details omitted in the original description, I will only present a superficial overall descripton here.

Body form as in figure 238. Total length 9.2 mm. (based on an average of 3 specimens). Greatest width 3.1 mm. (measured at widest part of genital segment). Dorsal thoracic plates present on segment 4. Genital segment about one-half body length. Abdomen 1-segmented and with broad dorsal plate. Caudal ramus broad, with 4 terminal naked setae.

Oral area (fig. 239) and associated appendages well described by Shiino except that it is worth noting that there is an adhesive pad between the bases of the maxillipeds as in *D. heptatus*.

Legs 1–4 biramose, with spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:1	0:1	I:1	0:1	I:1	0:1
seg. 2	IV:3	3	IV:5	8	IV:5	5	III:5	4

Leg 5 (fig. 240) located ventrally near outer distal corner of genital segment and composed of a signle lobe bearing a short plumose seta. Leg 6 (fig. 241) located near junction of abdomen and genital segment and represented by a finger-like lobe.

Egg strings coiled and not protruding (fig. 242), remaining hidden between dorsal abdomen plate and abdomen.

Color in preserved specimens cream and devoid of pigmentation.

MALE.—Unknown.

DISCUSSION.—I have been able to supplement the original description on a few points, particularly the nature of the 5th and 6th legs and the egg strings. The specimens I received were still attached to pieces of fin from the host shark. I noticed that the copepods were attached to the lighter pigmented surface (presumably lower) of the fin. This would indicate that in this instance the pectoral or pelvic fins were involved.

This is only the second record of this copepod; consequently, too little is known about the species to draw any conclusions regarding its host specificity or geographic distribution.

This species is easily separated from *D. heptatus* by the nature of the abdomen and general configuration of the body.

Genus *Pagina* Cressey, 1964

Pagina Cressey, 1964, p. 285. [Type-species: *P. tunica.*]

FEMALE.—Frontal plate distinctly separate. First thoracic segment fused with cephalon. Thoracic segments 2–4 free. Second and third thoracic segments without dorsal plates. Fourth segment with a dorsal plate. Abdomen 2-segmented, each segment with a dorsal plate. Abdomen attached to distal end of genital segment and visable dorsally. Cephalic appendages of typical pandarid type. Legs 1–4 biramose; rami of leg 1 2-segmented, those of legs 2–4 3-segmented; all bearing plumose setae. Fifth and sixth legs present. Egg sacs long.

MALE.—Body of typical pandarid form. No dorsal plates present. Appendages with same generic characters as the female.

The name *Pagina*, from Latin, meaning "a page," refers to the relationship of the abdominal plates to each other.

Pagina tunica Cressey, 1964

FIGURES 243–267

Pagina tunica Cressey, 1964, p. 285.

SPECIMENS STUDIED.—21 specimens (18 females and 3 males) collected from *Alopias superciliosus* (Lowe) caught at Majunga, Madagascar. Holotype female, allotype male, and 8 paratype females in alcohol deposited in the U.S. National Museum, 3 paratype females in alcohol deposited in the Collection of the Centre d'Oceanographic et des Peches de Nosy Bé, Madagascar, and the remaining paratypes in the author's collection.

OTHER SPECIMENS STUDIED.—A single collection from *Alopias superciliosus* from Nosy Bé, Madagascar; a single collection from the same host in the Pacific (0°38′N, 124°23′W).

FEMALE.—Body form as in figures 243 and 244. Total length, based on an average of 4 specimens, including caudal rami but not setae, 17.9 mm. Greatest width (measured at the widest part of cephalon) 5.8 mm.

Cephalon nearly round, slightly longer than wide, measuring 6.0 by 5.8 mm (measurements including marginal fringe). Posterior corners of cephalon projecting distally. First thoracic segment fused with head. Second segment distinct with 2 lateral lobes extending to posterior margin of third thoracic segment, thus incorporating the smaller third segment within its posterior border. Fourth thoracic segment with dorsal plate consisting of 2 conspicuous winglike lobes. The distal corner of this plate extends only slightly over anterior corner of genital segment. Genital segment large, its greatest length 4.6 mm and its greatest width at the posterior corners 3.8 mm. Posterior corners produced to form 2 short lobes. Abdomen 2-segmented, both segments possessing a conspicuous dorsal plate. From the dorsal aspect abdominal plates covering rest of abdomen. Ventrally the first abdominal segment (fig. 248) as wide as long, measuring 1.5 by 1.5 mm. Dorsal plate of this segment extending over rest of abdomen and with a deep median sinus dividing it into 2 long lobes (see figs. 243, 244). Second abdominal segment also as long as wide and measuring ventrally 2.1 by 2.1 mm. Its dorsal plate composed of only a single lobe and extending over proximal ends of caudal rami (see figs. 243, 245). Caudal ramus (fig. 245) large, comprising almost one-fourth of total body length. Each ramus about 4 times as long as wide measuring 4.2 by 1.3 mm. Distal end of ramus bearing 6 setae. The outermost and innermost small and naked, but median 4 plumose and all nearly equal in length, longest measuring 0.4 mm. Outer border heavily sclerotized while inner only weakly so and often appearing wrinkled in preserved specimens.

Oral area as in figure 246. A single pair of adhesion pads near base of first antenna. First antenna (fig. 247) 2-segmented. First segment 0.77 mm long and bearing 23 stout setae along anterior distal border, all of which are covered with spinules. Four smaller finely plumose setae internal to outer spines. Terminal segment 0.42 mm long and bearing 13 naked setae. Second antenna (fig. 249) 3-segmented. Terminal segment in form of a stout, heavily sclerotized claw bearing 2 setae, 1 basal and the other median. No adhesion pad associated with this appendage. Mouth tube (fig. 250) about twice as long as basal width with labium extending beyond tip of labrum. Tip of labrum somewhat expanded and weakly trilobed with a pair of subterminal processes projecting within tube (fig. 251). The labium expanded at tip and fringed as in figure 251. The mandible attached to head near base of tube (see fig. 250) and bearing a long process with extends between labrum and labium. Distal end of mandibular process with an inner row of about 11 teeth (fig. 252). First maxilla (fig. 253) indistinctly divided into 2 segments. Proximal segment with a group of 3 setae near base. Distal segment short and terminating as a blunt process. Second maxilla (fig. 254) 3-segmented. Second segment bearing a group of stout setules and a single seta at inner distal corner. Third segment short, with 2 transverse rows of setules and bearing a claw ornamented on proximal two-thirds of concave margin with transverse rows of spinules and on convex surface with longitudinal rows of spines. Maxilliped (fig. 255) apparently 4-segmented. First segment bearing padlike process on anteroventral surface, which undoubtedly serves as an adhesion pad. Third segment bearing a heavily sclerotized spinelike process opposed by claw of fourth segment, thus forming a chela. Fourth segment bearing a single seta near base of claw.

Legs 1–4 biramose, with spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:1	0:1	I:1	0:1	I:1	0:1
seg. 2	III:4	3	I:1	0:2	I:1	0:2	I:1	0:2
seg. 3	–	–	III:5	6	III:5	4	III:5	3

Leg 1 (fig. 256) with both rami 2-segmented. First exopod segment outwardly greatly inflated and bearing a single outer spine. Last exopod segment with 3 outer spines and 4 inner setae. First endopod segment with no setae but second segment bearing 3 setae. Basipodite bearing a short outer seta; inner margin naked except for a short seta. No setae on coxopodite. Leg 2 (fig. 257) with both rami 2-segmented. First exopod segment with an outer spine and an inner seta. Second segment same. Third segment with 3 outer spines and 5 terminal setae. First endopod segment with an inner seta. Second segment

with 2 inner setae. Third segment with 6 terminal setae. Basipodite with only an outer seta; inner margin with a row of hairs. Coxopodite seta stout and densely plumose. Leg 3 (fig. 258) with both rami 3-segmented. First and second exopod segments with an outer spine and an inner seta. Third segment with 3 outer spines and 5 terminal setae. First endopod segment with an inner seta. Second segment with 2 inner setae. Third segment with 3 terminal setae. Inner portion of basipodite expanded with a marginal fringe as in figure. No seta on the coxopodite. All setae on legs 1–4 plumose and all spines fringed. Leg 5 located on ventral surface near posterior corner of genital segment (see fig. 248), bearing 3 naked spines. Leg 6 modified to form a hooklike process that holds spermatophores in place (see fig. 248). Egg strings long, 1.5 times as long as body.

Male.—Body form as in figure 260. Total length, based on an average of 2 specimens, including caudal ramus but not setae 11.7 mm. Greatest width 4.6 mm measured at widest part of cephalon. Cephalon nearly round somewhat wider than long (4.6 by 4.2 mm) with posterior corners projecting. Lateral dorsal edge of segment 2 bearing on each side a clear membrane that extends posteriorly to fourth segment. Fourth segment with only a suggestion of winglike plate found in female. Genital segment (fig. 261) 2.6 by 2.1 mm, somewhat longer than wide. Spermatophores visable through posterior half of genital segment. Abdomen 2-segmented, without dorsal plates. First segment measuring 0.88 by 0.88 mm. Second segment longer than wide (1.4 by 1.08 mm) with widest part in distal portion of segment. Caudal ramus armed as in female; about 4 times as long as wide (1.9 by 0.49 mm). Inner margin bearing a row of short hairs.

Oral area as in female. First antenna like that of female. Second antenna (fig. 262) 4-segmented. Second segment with striated areas as shown in figure. Claw shorter and stouter than in female and composed of 2 segments (in the female these segments are fused to form 1). Other oral appendages like those of female. Maxilliped (figs. 263, 264) heavily sclerotized with a chela at tip. When chela is closed, claw of last segment fits into a bifurcation on tip of spinelike process on penultimate segment. A bossed area present between these claws. In addition to claw, last segment bearing a single seta (see fig. 264). Adhesion process near base of maxilliped as in female.

Legs 1–4 as in female except for last endopod segment of leg 3 (fig. 265). Ventral surface of this segment bearing a heavily sclerotized process that extends out over an embossed area near edge (this seems to be modified for holding, but exact function is yet unknown). In addition to ventral process, a more weakly sclerotized dorsolateral process. Leg 5 (fig. 266) located ventrolaterally in middle of genital segment (see fig. 261) and bearing 4 setae, 3 plumose and 1 fringed with

spinules. Outer seta not greatly displaced from other 3, as in female. Leg 6 (fig. 267) located internal to distal corner of genital segment and consisting of a small process bearing short setae.

Discussion.—The genus *Pagina* is closely related to *Dinemoura* Latreille, 1829, of which there are 4 known species. These 2 genera have the following characteristics of the female in common: a wing-like dorsal plate on the fourth thoracic segment; a 2-segmented abdomen, each abdominal segment bearing a dorsal plate, the first of which is bilobed and the second single-lobed, and legs 1–3 similar and relatively unmodified. *Pagina* can be separated from *Dinemoura* by the fact that in *Dinemoura* the fourth leg is broad and conspicuously lamelliform, whereas the fourth leg of *Pagina* is unmodified.

Pagina is unlike all other known genera of this family in having the rami of legs 2–4 3-segmented.

Genus *Echthrogaleus* Steenstrup and Lütken, 1861

Dinemoura.—Guerin-Meneville, 1837, pl. 35. [Refers to *D. alata* only.]
Dinematura.—Dana, 1852, p. 60. [Refers to *D. braccata* only.]
Echthrogaleus Steenstrup and Lütken, 1861, p. 380. [Type-species: *E. coleoptratus.*]
Pandarus.—Thomson, 1889, p. 363. [Refers to *P. armatus* only.]

Female.—Frontal plate distinctly separate. First thoracic segment fused with cephalon. Dorsal thoracic plates on segment 4. Abdomen 1-segmented. Abdomen concealed beneath genital segment. Caudal rami joined to abdomen terminally. Oral adhesion pads present but somewhat reduced. First antenna 2-segmented. Legs 1–4 biramose. Leg 4 lamelliform. Legs 5 and 6 present. Egg strings long and straight.

Male.—No dorsal thoracic plates present. Abdomen 2-segmented Legs 1–4 biramose. Leg 3 with modification on endopod. Leg 4 not lamelliform. Legs 5 and 6 present and not as reduced as in female. Other oral and thoracic appendages as in the female.

Discussion.—This genus is cosmopolitan as a parasite on the body surface of elasmobranch fishes. *E. coleoptratus* and *denticulatus* may be restricted to larger pelagic sharks whereas *torpedinis* has been reported only from the ray, *Torpedo occidentalis.* The copepod is parasitic on the body surface of the host.

This genus is closely related to *Dinemoura* but differs from it principally in having a 1-segmented abdomen. The males of this genus have not been well described. The descriptions of *coleoptratus* and *denticulatus* males have been amplified here.

In 1899 Thomson described a copepod under the name of *Dinematura hamiltoni.* This is obviously a member of the genus *Echthrogaleus,* but the figures and description are too poor to assign it to any species.

Key to Females of Genus *Echthrogaleus*

1. Posterior border of dorsal thoracic plate smooth. Leg 5 concealed in dorsal view . . . . . **coleoptratus**
   Posterior border of dorsal thoracic plate serrate 2
2. Leg 5 visible in dorsal view. Dorsal thoracic plate covering not more than ½ genital segment . . . . . **denticulatus**
   Leg 5 concealed in dorsal view. Dorsal thoracic plate covering at least ⅔ genital segment . . . . . **torpedinis**

Echthrogaleus coleoptratus (Guerin-Meneville, 1837)

FIGURES 264–280

Dinemoura alata Guerin-Meneville, 1837, p. 42.
Dinemoura coleoptrata Guerin-Meneville, 1837, p. 42.
Dinemoura affinis Milne-Edwards, 1840, p. 465.
Dinematura braccata Dana, 1852, p. 60.
Echthrogaleus coleoptratus Steenstrup and Lütken, 1861, p. 380.—Olsson, 1868, p. 20.—Norman, 1868, p. 301.—Rathbun, 1884, p. 488.—Brian, 1899, p. 4; 1902, p. 8; 1906, p. 53; 1908, p. 4; 1912, p. 12; 1914b, p. 148; 1944, p. 202.—Bassett-Smith, 1899, p. 464.—Scott, T., 1900, p. 156; 1901, p. 125; 1902, p. 292.—Scott, T., and Scott, A., 1913, p. 89.—Norman and Scott, T., 1906, p. 214.—Wilson, 1907, p. 367; 1908, p. 452; 1920, p. 12; 1922, p. 5; 1923, p. 13; 1932, p. 427.—Norman and Brady, 1910, p. 404.—Stebbing, 1910, p. 559.—Hansen, 1923, p. 33.—Marukawa, 1925, p. 1242; 1947, p. 926.—Yamaguti, 1936, p. 7; 1963, p. 119.—Oorde and Schuurmans Stekhoven, 1936, p. 139.—Rose and Vaissiere, 1953, p. 86.—Shiino, 1954, p. 291; 1957, p. 364.—Delamare-Debouteville and Nunes-Ruivo, 1954, p. 204.—Barnard, 1955, p. 264.—Capart, 1959, p. 97.—Stuardo and Fagetti, 1961, p. 58.—Heegaard, 1962, p. 177.
Echthrogaleus braccatus.—Heller, 1868, p. 197.—Thomson, 1889, p. 361.—Norman and Scott, 1906, p. 213.—Wilson, 1907, p. 366.
Nogagus lutkenii Norman, 1868, p. 300.
Echthrogaleus perspicax Olsson, 1868, p. 18.—Wilson, 1907, p. 457.
Echthrogaleus lutkenii.—Norman and Scott, 1906, p. 213.—Scott, T., and Scott, A., 1913, p. 90.—Oorde and Schuurmans Stekhoven, 1936, p. 139.
Echthrogaleus affinis.—Brady, 1883, p. 133.—Bassett-Smith, 1899, p. 465.—Wilson, 1907, p. 363.

SPECIMENS STUDIED.—Twenty-six collections from *Prionace glauca* from the western North Atlantic (35°–45°N, 20°–80°W). A single collection from *Lamna ditropis* Hubbs and Fallett sent to me by Dr. P. Gilbert from the North Pacific. Four collections from *Prionace glauca* from the Indian Ocean (42°23′S, 74°56′E) and 2 collections from *Lamna nasus* (Bonnaterre) at the same locality.

This copepod has been extensively collected and reported in the literature. The female has been well described and figured (most recently by Shiino, 1954); however, the male is poorly known and will be dealt with here in more detail.

FEMALE.—Body form as in figure 268. Total length 9.7 mm (based on an average of 10 specimens). Greatest width 4.8 mm. Dorsal

thoracic plates on segment 4. Oral area and associated appendages described by Shiino (1954). First maxilla as in figure 269. Adhesion pads present but small.

Leg 1–4 biramose with spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:1	0:1	I:1	0:1	X	IV
seg. 2	IV:3	3	I:0	8	I:1	6		
seg. 3			III:5		III:5			

Leg 1 endopod (fig. 270) with usual 3 setae but inner and outer short. Sternal plate between legs 1 with a bilobed adhesion pad (fig. 271). Leg 5 (fig. 272) a single lobe with 3 stout spines near tip. Leg 6 incorporated into area of spermatophore attachment and not a separate element.

Egg strings long and straight.

Color in life cream with light brown pigment on cephalon.

MALE.—Body form as in figure 273. Total length 6.4 mm (based on an average of 2 specimens). Greatest width 3.6 mm (measured at widest part of the cephalon). Cephalon rounded, about as long as wide. No dorsal plates present. Genital segment (fig. 274) 1.6 by 1.4 mm, slightly longer than wide. Posterior corners not markedly produced. Abdomen 2-segmented. Caudal ramus with 4 moderately long, plumose setae and plumose along inner margin.

Oral area and associated appendages as in the female. Adhesion pads somewhat smaller.

Legs 1–4 biramose. Spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:1	0:1	I:1	0:1	I:1	0:1
seg. 2	IV:3	3	I:1	8	I:1	II:6	I:1	5
seg. 3			III:5		III:5		II:5	

Leg 1 (fig. 275) as in the female except that setae on endopod are of equal length in male. Leg 2 (fig. 276) as in female but without patches of stout spinules. Leg 3 with a modification of last endopod segment (fig. 277). Leg 4 as in figure 278.

Leg 5 (fig. 279) located on midlateral margin of genital segment and consisting of a single lobe with 1 stout spine and 3 plumose setae. Leg 6 (fig. 280) situated near junction of genital segment and abdomen and represented by a single spine and plumose seta.

Color in life cream, devoid of pigment.

DISCUSSION.—*Echthrogaleus coleoptratus* is a widely distributed species of copepod and has been reported from a wide variety of sharks. It is generally found on pelagic rather than inshore varieties. It occurs on the body surface of the host, commonly on the fins.

The male shows the modified endopod of leg 3 placing this copepod in group II.

Echthrogaleus denticulatus Smith, 1874

FIGURES 281–290

Echthrogaleus denticulatus Smith, 1874, p. 282.—Rathbun, 1884, p. 488.—Wilson, 1907, p. 369; 1932, p. 428.—Shiino, 1954, p. 297; 1959b, p. 352.

Dinematura neozealanica Thomson, 1889, p. 359.—Bassett-Smith, 1899, p. 464.—Wilson, 1907, p. 363.

Pandarus armatus Thomson, 1889, p. 363. [*Nogagus* male.]

SPECIMENS STUDIED.—A single large collection from *Alopias pelagicus* Nakamura from Majunga, Madagascar. Three collections from *Alopias vulpinus* from the Indian Ocean (16°13′N, 63°29′E; 9°24′N, 54°58′E; 7°17′N, 55°00′E). A single collection from *Eulamia floridanus* from the Indian Ocean (14°36′N, 55°23′E). Two collections from *Alopias vulpinus* from the Pacific Ocean (7°47′N, 102°37′W; 11°15′N, 113°26′W).

FEMALE.—Body form as in figure 281. Total length 7.8 mm (based on an average of 5 specimens). Greatest width 4.3 mm (measured at the widest part of cephalon). The female of this species has been recently redescribed and figured by Shiino (1954) and a complete description will not be repeated here. Oral area of usual type, adhesion pads present. Cephalic appendages as shown by Shiino except terminal claw of second maxilla (fig. 282) is indistinctly subdivided.

Legs 1–4 biramose with spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:1	0:1	I:1	0:1	X	VI
seg. 2	IV:3	3	I:1	0:2	I:1	6		
seg. 3			IV:4	6	III:5			

Leg 5 (fig. 283) a long process projecting beyond distal corners of genital segment, bearing a stout terminal spine and 2 subterminal setae. Leg 6 (fig. 284) located at junction of abdomen and genital segment and composed of a bilobed process. Leg 6 covered by abdomen in ventral view.

Egg strings long and straight.

Color in life cream, no pigmentation.

MALE.—Body as in figure 285. Total length 5.2 mm (based on an average of 2 specimens). Greatest width 2.8 mm (measured at widest point of cephalon). Frontal plate separate. Cephalon rounded, somewhat wider than long. No dorsal thoracic plates. Genital segment (fig. 286) with posterior corners produced only slightly. Two patches of spinules on ventral surface of segment. Genital segment longer than wide (1.2 by 1.0 mm). Abdomen 2-

segmented. First segment 218μ long. Second segment 360μ long. Caudal rami long, measuring 720μ by 144μ (about 5 times as long as wide). Each ramus bearing 4 plumose terminal setae and 2 shorter subterminal ones. Each ramus plumose along inner edge.

Oral area as in female. Setae on first and second antennae slightly longer than in female.

Legs 1–4 biramose with spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:1	0:1	I:1	0:1	I:1	0:1
seg. 2	IV:3	3	I:1	8	I:1	II:6	I:1	5
seg 3			III:5		III:5		III:4	

Leg 1 as in female. Leg 2 endopod of only 2 segments. Leg 3 with modification as in figure 287. Leg 4 (fig. 288) bearing a prominent spine on outer distal corner of first exopod segment. Leg 5 (fig. 289) located on posterior corners of genital segment, composed of a process bearing a stout terminal spine and 3 setae on inner margin. Distal 2 setae plumose. Proximal one naked. Leg 6 (fig. 290) located at junction of abdomen and genital segment, composed of an inner stout spine and an outer plumose seta.

Color in life cream and devoid of pigment.

Discussion.—This copepod was recently redescribed by Shiino (1954). He described a male of this species also, but a closer examination shows this to be actually the male of *Pandarus satyrus*. A comparison of his description and figures leaves no doubt as to its true identity. He comments that there is "a remarkable dimorphism found between the sexes." This is not the case when one considers the true male of this species, described here for the first time. The modification on the third leg is well formed, establishing the position of this species in group II. I have synonymized *D. neozealanica* Thomson, 1889, with this species since Thomson's original description fits in every way.

This copepod is found generally on the body surface of a wide variety of pelagic sharks. It is occasionally recovered from the gills also. I collected large numbers of this species from *Alopias vulpinus* in the Indian Ocean. On this host the copepod often occurred in great clusters (200–300 copepods) around the opening of the cloaca. Females far outnumber the males in such cases. This copepod has been reported from the Atlantic (Smith, 1874), North Pacific (Shiino, 1954), and I have collected it from the Indian Ocean and received material from the Central Pacific. This seems to indicate a cosmopolitan distribution. It is apparently a common parasite of the genus *Alopias*.

Echthrogaleus torpedinis Wilson, 1907

FIGURES 291–294

Echthrogaleus torpedinis Wilson, 1907, p. 371; 1932, p. 429.

SPECIMENS STUDIED.—USNM 11350, syntypes. 3 females from *Torpedo occidentalis* from Provincetown, Mass.

The only material available for study were type specimens from the U.S. National Museum. Because I did not dissect any of these types, a complete redescription is not possible here. This will have to wait until more material can be collected; nevertheless, I have figured some details and have added here to the original description.

FEMALE.—Body form as in figure 291. Total length 12.8 mm (based on a single specimen). Greatest width 8.2 mm (measured at widest part of the dorsal thoracic plates). Cephalon rounded, about as wide as long (6.2 by 6.2 mm). Dorsal thoracic plates on segment 4. These plates very conspicuous and serrated along their posterior borders. Plates extending over the proximal two-thirds of the genital segment. Genital segment with its posterior corners produced to form inwardly directed lobes. Abdomen 1-segmented, hidden in dorsal view. A small dorsal plate with abdomen. Caudal ramus (fig. 292) bearing 6 naked setae on posterior border. Rami with fine spinules along inner margins.

Oral area with adhesion pads reduced. Pad associated with maxilliped in form of a posteriorly directed process. Oral appendages like those of *E. denticulatus*.

Legs 1–4 (fig. 293) biramose with spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:1	0:1	I:1	0:1	IX	IV
seg. 2	IV:3	3	I:1	7	I:1	6		
seg. 3			IV:4		IV:4			

Leg 4 lamelliform as in figure. Leg 5 (fig. 294) a process not projecting beyond tip of genital segment, bearing a single stout spine and 3 setae armed as in figure. Leg 6 as in *E. denticalatus*.

Color in preserved specimens cream tan, devoid of heavy pigmentation.

Egg strings long and straight.

MALE.—Unknown.

DISCUSSION.—This species seems closely related to *E. denticulatus*, but it can be separated from that species by the nature of the dorsal thoracic plates of segment 4, by the relative length of leg 5, and by the differences in the armature of the legs. This copepod has been collected twice from *Torpedo occidentalis* off the coast of Massachusetts. Further collecting would be necessary before concluding that

it is specific to that host. It was reported by Wilson (1907) from the pectoral and ventral fins of the host.

Genus *Nesippus* Heller, 1868

Nesippus Heller, 1868, p. 193. [Type-species: *N. orientalis*.]
Nogagus.—Beneden, 1892b, p. 246. [Refers to *N. augustatus* only.]

Female.—Frontal plate distinctly separate. First thoracic segment fused with cephalon. Thoracic segments 2–4 free. Dorsal plate may or may not be present on segment 4. Abdomen 1-segmented and joined to genital segment ventrally. Caudal rami attached distally to abdomen. Adhesion pads present on cephalon. First antenna 2-segmented. Oral appendages of usual pandarid type. Maxilliped with a claw pointed or rounded at tip. Legs 1–4 biramose. Rami of legs 1–3 2-segmented, those of leg 4 1-segmented. Leg 5 reduced to 1 or 2 setae. Leg 6 absent. Egg strings straight.

Male.—The same generic characters of female with following exceptions. A reduced modification on endopod of leg 3. Leg 6 present but much reduced. Abdomen 1-segmented. The males of this genus can be separated from all other pandarids by the 1-segmented abdomen.

Discussion.—Members of this genus seem to be restricted to inshore species of sharks and are generally not found on the body surface of the host. The usual sites of infestation are the mouth, gill arches, and nasal passages.

Three species of copepods have been described and assigned to the genus *Nesippus* that are now certainly not members of this genus: *Nesippus curticaudis* Dana, 1852, *N. borealis* Steenstrup and Lutken, 1861, and *N. bengalensis*, Gnanamuthu, 1949. These are described as males of this genus. On the basis of the descriptions of the males of 2 species of *Nesippus* in this paper, it has been shown that the above 3 species are not males of this genus. None of these species shows any indication of sexual maturity. None has been reported in copulation with a female. All have been reported from the plankton. These 3 species, therefore, should be removed from this genus. Their taxonomic position remains in doubt owing to the fact that they appear to be immature. It cannot be established that they are even members of the family Pandaridae.

Key to Adult Females of Genus *Nesippus*

1. Endopod of leg 4 unarmed 2
   Endopod of leg 4 with long setae 3
2. Genital segment conspicuously narrowed anteriorly, caudal rami with prominent setae . . . . . **crypturus**

Genital segment not conspicuously narrowed anteriorly, caudal rami with small reduced setae . . . . . **tigris**

3. Fourth thoracic segment with alate plates . . . . . **orientalis**
   Fourth thoracic segment without plates . . . . . **vespa**

Nesippus orientalis Heller, 1868

FIGURES 295–304

Nesippus orientalis Heller, 1868, p. 194.—Bassett-Smith, 1899, p. 459.—Brian, 1906, p. 49; 1924, p. 33.—Wilson, 1907, p. 457.—Capart, 1953, p. 658; 1959, p. 96.—Rose and Vaissiere, 1953, p. 86.—Barnard, 1955, p. 265.—Nunes-Ruivo, 1956, p. 22.—Yamaguti, 1963, p. 123.

Nogagus angustatus Beneden, 1892b, p. 245.

Nesippus alatus Wilson, 1905, p. 130; 1907, p. 426; 1932, p. 438.—Bere, 1936, p. 595.—Heegaard, 1943b, p. 27.—Pearse, 1952b, p. 213.—Capart, 1953, p. 659.—Rose and Vaissiere, 1953, p. 86.—Barnard, 1955, p. 265.—Yamaguti, 1963, p. 123.

Nesippus ornatus Thomsen, 1949, p. 17.—Yamaguti, 1963, p. 124.

Nesippus incisus Heegaard, 1962, p. 179.

Nesippus australis Heegaard, 1962, p. 178.

SPECIMENS STUDIED.—Five collections from Sarasota, Fla., from the following hosts: *Ginglymostomum cirratum*, *Galeocerdo cuvier*, *Carcharinus leucas*, and *Carcharinus maculipinnis*. A single collection from *Sphryna zygaenae* from Durham, South Africa. From Nosy Bè, Madagascar, the following: 8 collections from *Carcharinus maculipinnis*, 4 collections from *Sphyrna lewini*, 4 collections from *Carcharinus leucas*, 1 collection from *Galeocerdo cuvier*, and 1 collection from *Scoliodon palasorrah*.

FEMALE.—Body form as in figure 295. Total length 5.6 mm (based on an average of 5 specimens). Greatest width 3.1 mm (measured at widest point of cephalon). Cephalon rounded about as long as wide. Thoracic segments 2–4 free with dorsal plates on segment 4. Plates extending posteriorly slightly over anterior portion of genital segment. Genital segment 2.1 mm long and 1.5 mm wide. Genital segment of equal width throughout with posterior border trilobed. Abdomen (fig. 296) 1-segmented. Caudal rami (see fig. 296) with 6 terminal setae, inner 4 plumose.

Oral area with adhesion pads associated with first and second antennae and maxilliped. The pad of first antenna with posterior margin produced to form a hooklike process (fig. 297). First antenna 2-segmented (see fig. 297). Second antenna clawlike; of usual pandarid form. Mandible with 11 teeth at tip and of usual type. First maxilla (fig. 298) with a broad process on outer distal corner. Second maxilla (fig. 299) with tip produced to form a clear bulblike tip. A short plumose spine and a small patch of hairs near base of claw. Maxilliped (fig. 300) with a short blunt claw.

Legs 1–4 biramose with spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:1	0:1	I:0	0:1	V:4	4
seg. 2	IV:3	3	IV:5	7	IV:5	4		

Leg 1 (fig. 301) with an interpodal adhesion pad as in figure. Leg 2 (fig. 302) armed as in figure. Leg 3 (fig. 303) with innermost seta of last exopod segment reduced. Leg 4 (fig. 304) with each ramus 1-segmented and armed as in figure. Leg 5 small process bearing 2 short setae (see fig. 296). Leg 6 absent.

Egg strings long and straight.

Color in life cream.

MALE.—Wilson in 1905 described a male of *Nesippus alatus* (=*orientalis*). I have examined this type specimen and have concluded that it is immature and does not indicate the nature of the adult male; consequently, the true adult male of this species is unknown.

DISCUSSION.—This copepod has been reported from a number of sharks and is probably cosmopolitan in distribution. It seems to be restricted to inshore species and is usually found in the mouth and gill arches of the host.

Capart (1953) states that more material will eventually show *alatus* and *angustatus* to be synonymous with *orientalis*. As a result of my collections and the material I have examined, I am convinced that this interpretation is correct and have placed the two former in synonymy. *Nesippus ornatus* described by Thomsen in 1949 is also the same as *orientalis*. Heegaard described 2 new species (*incisus* and *australis*) in 1962. He noted the similarity to *alatus* and *orientalis* and I believe that these 2 species should be placed in synonymy. I have examined material from the North Atlantic, Caribbean, and Indian Ocean and conclude that my own collections represent a single cosmopolitan species that is found on a wide variety of hosts. The exact shape of the dorsal thoracic plates of segment 4 should not be regarded by itself as a specific character. The presence of this plate separates it from the other known species. It also differs from other species in the nature of the adhesion pad of the first antenna.

Nesippus crypturus Heller, 1868

FIGURES 305–324

Nessipus crypturus Heller, 1868, p. 196.—Bassett-Smith, 1899, p 459.—Wilson, 1907, p. 425; 1935a, p. 3.—Barnard, 1955, p. 265.—Yamaguti, 1963, p. 124.
Nesippus occultus Wilson, 1924b, p. 214.—Yamaguti, 1963, p. 124.
Nesippus costatus Wilson, 1924b, p. 213.—Yamaguti, 1963, p. 124.
Nesippus gracilis Wilson, 1935a, p. 4.—Bere, 1936, p. 595.—Yamaguti, 1963, p. 124.

SPECIMENS STUDIED.—Single collections from Sarasota, Fla., from the following hosts: *Sphryna mokarran*, *Galeocerdo cuvier*, *Carcaharinus milberti*, and *Carcharinus leucas*. A single collection from Socorro Island (Pacific) from *Carcharinus galapagensis*. From Nosy Bé Madagascar: *Sphyrna lewini* (4 collections), *Carcharinus maculipinnis* (8 collections), *C. leucas* (4 collections), *Scoliodon palasorrah* (1 collection), and *Galeocerdo cuvier* (1 collection).

FEMALE.—Body form as in figure 305. Total length 6.8 mm (based on an average of 5 specimens). Greatest width 3.5 mm (measured at widest part of cephalon). Cephalon rounded, somewhat wider than long (2.5 by 2.7 mm). Thoracic segment 2 expanded laterally. Segment 3 small. Segment 4 expanded laterally somewhat but no plates present. Genital segment 2.6 mm long and narrowed anteriorly; posterior border with deep median sinus. Abdomen (fig. 306) 1-segmented Caudal rami (see fig. 306) attached to abdomen distally and with 6 terminal setae, inner 4 plumose and longer than outer 2.

Oral area with adhesion pads associated with first and second antennae and maxilliped (see fig 307). First antenna (fig. 308) 2-segmented, armed as in figure. Adhesion pad produced to form a hooklike process. Second antenna (see fig. 307) of usual form. Mandible and mouth tube of usual form. First maxilla (fig. 309) a broad lobe with a small outer spine and an anterior group of 3 setae. Second maxilla of usual type. Maxilliped (fig. 310) with a short terminal claw rounded at tip. Tip of claw is opposed by a raised area with a central crater-like depression.

Legs 1–4 biramose with the spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:1	0:1	I:1	0:1	V	0
seg. 2	IV:3	3	IV:5	7	IV:4	4		

Terminal exopod segments of legs 1–3 (figs. 311–313) with spines armed as in figures. Setae of these legs pinched near base and often broken off at this point (see figs. 311–313). Leg 4 (fig. 314) with each ramus of 1 joint. Endopod unarmed. Leg 5 (fig. 315) consisting of 2 short setae, 1 naked, the other with a serrate fringe. Leg 5 located lateral to caudal rami on ventral surface of genital segment (see fig. 306). Leg 6 absent.

Egg strings long and straight.

Color in life cream.

MALE.—Body form as in figure 316. Total length 5.4 mm (based on an average of 2 specimens). Greatest width 3.1 mm (measured at widest part of cephalon). Lateral margins of thoracic segment 2 somewhat alate. No dorsal plates present. Genital segment slightly

longer than wide. Abdomen 1-segmented. Caudal rami (fig. 317) with 4 terminal setae and 2 subterminal. Each ramus joined distally to abdomen.

Oral area with adhesion pads as in female. First antenna as in female. Second antenna (fig. 318) with terminal hook more recurved than in female. An adhesion area present on antepenultimate segment. Remaining oral appendages as in female. Maxilliped with tip of terminal claw produced as in figure 319. Legs 1–4 (figs. 320–323) biramose with spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:0	0:1	I:1	0:1	IV:4	4
seg. 2	IV:3	3	IV:5	7	IV:4	4		

Leg 5 (fig. 324) located near outer distal corner of genital segment and consisting of 2 short, naked setae. Leg 6 absent.

Discussion.—This species, like *N. orientalis*, seems to be cosmopolitan in distribution and occurs in the mouth and gill arches of a variety of inshore species of sharks.

The copepod was originally described by Heller in 1865 and has since been redescribed as *N. occultus*, *N. costatus*, and *N. gracilis* by C. B. Wilson (1924; 1924b; 1935). I have examined Wilson's types of *N. gracilis* and determined this to be the same as *N. crypturus*. *Nesippus occultus* from the published description also appears to be synonymous. *Nesippus costatus* was described from an immature female and was collected together with the material described as *N. occultus* by Wilson. It appears to be merely a young female of the type described as *N. occultus*.

This copepod is characterized by a lack of dorsal plates, the nature of the fourth leg of the female, and the deep median sinus on the posterior portion of the female genital segment. The form of the male maxilliped should separate this sex from other species of the genus.

Nesippus tigris, new species

Figures 325–345

Specimens studied.—Twelve females and 4 males from *Galeocerdo cuvier* from Sarasota, Fla. Holotype female, allotype male, 3 paratypes (2♀♀, 1♂) deposited in alcohol in the U.S. National Museum. Four paratypes (females) deposited in the British Museum (Natural History). Remaining paratypes in the author's collection. Additional specimens studied from *Galeocerdo cuvier* from Nosy Bé, Madagascar (6♀♀).

Female.—Body form as in figure 325. Total length 8.2 mm (based on an average of 2 specimens). Greatest width 4.3 mm (measured at widest part of cephalon). Cephalon rounded, slightly

wider than long (4.1 by 4.3 mm). Thoracic segments 2–4 free. No dorsal plates present but lateral margins of segments 2 and 4 expanded laterally somewhat. Genital segment 3.9 by 2.9 mm, widest at its midpoint, its lateral margins somewhat irregular. Genital segment with a median sinus posteriorly. Abdomen (fig. 326) 1-segmented. Caudal rami (see fig. 326) round, bearing 3 weak spines as in figure.

Oral area with adhesion pads associated with first and second antennae and maxilliped. First antenna (figs. 327, 328) 2-segmented.

Each segment armed as in figures. All spines and setae of first antenna naked. Adhesion pad of first antenna produced to form a sharp, posteriorly directed spine (see fig. 327). Second antenna (fig. 329) of usual form with 2 short setae on distal claw. Mouth tube and mandible as in other members of genus. First maxilla (fig. 330) with a median short, stout spine and an anterior group of 3 short setae. Second maxilla (fig. 331) with a short terminal claw bearing rows of fringe. The penultimate segment with a stout distal spine and a small patch of setae. Maxilliped (fig. 332) with a stout terminal claw opposed by a raised area with a central depression on penultimate segment. Maxilliped with an adhesion pad near base. Pad produced in form of a sharp, posteriorly directed process (fig. 333). This process seemingly subdivided.

Legs 1–4 biramose with spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:1	0:1	I:1	0:1	IV	0
seg. 2	IV:3	3	IV:5	7	IV:4	4		

Leg 1 (fig. 334) with both rami 2-segmented. Setae constricted near their bases as in *N. crypturus*. First exopod segment with an outer spine. Last exopod segment with 4 outer spines and 3 inner setae. First endopod segment unarmed. Last endopod segment with 3 terminal setae. Leg 2 (fig. 335) with both rami 2-segmented. First exopod segment with an outer spine and an inner seta. Last exopod segment with 4 outer spines and 5 inner setae. First endopod segment with an inner seta. Last endopod segment with 7 terminal setae. Leg 3 (fig. 336) with both rami 2-segmented. First exopod segment with an outer spine and an inner seta. Last exopod segment with 4 outer spines and 4 inner setae. First endopod segment with an inner seta. Last endopod segment with 4 terminal setae. Leg 4 (fig. 337) with both rami 1-segmented. Exopod with 4 terminal spines. Endopod unarmed. Leg 5 a single seta located on ventral surface of genital segment near posterior corner (see fig. 326).

Egg strings long and straight.

Color in life cream.

Male.—Body form as in figure 338. Total length 5.7 mm (based

on an average of 2 specimens). Greatest width 3.6 mm (measured at widest part of cephalon). No dorsal plates. Posterior corners of segment 2 produced. Genital segment about as long as wide (1.6 by 1.6 mm). Abdomen 1-segmented. Caudal ramus (fig. 339) somewhat rounded with 4 terminal plumose setae and 2 short subterminal ones. Inner margin with short hairs.

Oral area as in female. Appendages of cephalon as in female except for maxilliped. Maxilliped (fig. 340) with tip of claw papillose (fig. 341). Adhesion areas as in figure 340. Adhesive pad of maxilliped (fig. 342) not pointed as in female but with posterior portion produced as a rounded process with heavy striations as in figure.

Legs 1–4 biramose with spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg 1	I:0	0:0	I:1	0:1	I:1	0:1	IV:3	4
seg 2	IV:3	3	IV:5	7	IV:5	4		

Legs 1 and 2 as in female. Leg 3 with a modification on last endopod segment as in figure 343. This is consistent with group II males, although this modification is much reduced in this species. Leg 4 (fig. 344) with each ramus 1-segmented but not as reduced as the female. Leg 5 (see fig. 345) a single short seta on margin of genital segment. Leg 6 (see fig. 345) a single short seta near junction of genital segment and abdomen.

Discussion.—This species has been collected twice from *Galeocerdo cuvier*. The specimens from Nosy Bé were recovered from the nasal passages of the host. Those from Sarasota were not collected by the author, and there is no information as to their location on the host.

This species may be separated from *N. orientalis* by the nature of the fourth legs of the females. It seems to be more closely related to *N. crypturus* but can be separated from it on the basis of the caudal rami and by the fact that in *N. crypturus* the genital segment is considerably narrowed anteriorly whereas in *N. tigris* it is not markedly so.

The name *tigris*, from Latin, meaning "tiger," refers to the host, the tiger shark.

Nesippus vespa Kirtesinghe, 1964

Figures 346–356

Nessipus vespa Kirtesinghe, 1964, p. 91.

Specimens studied.—Eleven females form *Rynchobatus djeddensis* (Forskal) from Nosy Bé, Madagascar.

Female.—Body form as in figure 346. Total length 3.8 mm (based on an average of 2 specimens). Greatest width 1.5 mm (measured at widest part of cephalon). Cephalon rounded, slightly wider than long (1.2 by 1.5 mm). Thoracic segments 2 and 3 indistinctly divided

in dorsal view. No dorsal plates present. Genital segment globose, about as long as wide (1.3 mm long by 1.2 mm wide). Genital segment deeply incised posteriorly. Abdomen (fig. 347) joined distally to abdomen and bearing 6 terminal setae, inner 4 long and plumose. Inner margin of ramus with a row of hairs.

Oral area with adhesion pads as in other species of genus. Pad associated with first antenna not produced to form a hooklike process as in other species of the genus (see fig. 348). First antenna (fig. 348) 2-segmented, armed as in figure, and bearing only 12 spines on first segment and 6 setae on the second. Second antenna (fig. 349) of usual form. The 2 setae near base of claw longer than in other species of genus. Mouth tube and mandible of usual pandarid type. First maxilla (fig. 351) with a short spine and a small patch of setules near base of the claw. Claw with rows of fringe as in figure. Maxilliped (fig. 352) bearing a blunt terminal claw opposed by a crater-like area on opposite segment.

Legs 1–4 biramose with spine and setal formula as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp	end.	exp.	end.
seg. 1	I:0	0:0	I:1	0:1	I:1	0:1	IV:3	4
seg. 2	IV:3	3	IV:5	7	IV:4	4		

Leg 1 (fig. 353) with both rami 2-segmented. First exopod segment with an outer spine. Last exopod segment with 4 outer spines and 3 inner setae. First endopod segment unarmed. Last endopod segment with 3 terminal setae. Leg 2 (fig. 354) with both rami 2-segmented. First exopod segment with an outer spine and an inner seta. Last exopod segment with 4 outer spines and 5 inner seta. First endopod segment with an inner seta. Last endopod segment with 7 terminal setae. Leg 3 (fig. 355) with each ramus 2-segmented. First segment of the exopod with an outer spine and an inner seta. Last exopod segment with 4 outer spines and 4 inner setae. First endopod segment with an inner seta. Last endopod segment with 4 terminal setae. Leg 4 (fig. 356) with each ramus 1-segmented. Exopod with 4 outer spines and 3 inner setae. Endopod with 4 setae. Setae on legs 1–4 constricted near their bases (see fig. 355) and often broken off at this point. Leg 5 (see fig. 347) a single plumose seta located ventrally near distal margin of genital segment. Leg 6 absent.

Egg strings long and straight.

Color in life cream.

Discussion.—This copepod has been collected only from *Rhynchobatus djeddensis* in Madagascar and Ceylon. It was found in the mouth of the host in Madagascar and on the body surface of the Ceylon host.

This species can be separated from *N. orientalis* by the lack of the dorsal plate on fourth segment. It can be separated from *N. crypturus* by the nature of adhesion pads of the cephalon and the nature of the fourth leg of the female. It differs from *N. tigris* by the nature of the fourth thoracic segment (wide in *N. tigris*, narrow in *N. vespa*) and also by the nature of the caudal rami.

Genus *Paranesippus* Shiino, 1955

Paranesippus Shiino, 1955, p. 340. [Type-species: *P. incisus*.]

In 1955 Shiino described a new genus and species of parasitic copepod on the basis of a single female specimen taken from the body surface of *Acanthidium eglantina* (Jordan and Snyder).

In general, this copepod appears to be a member of group II and, as the name implies, seems to be more closely related to *Nesippus* than to other members of the family. Since Shiino has provided a good description with illustrations, I shall not repeat his description here. Because I had no material to study, I cannot add any more details to the existing description.

Adhesion pads are associated with first and second antennae and maxilliped.

The spine and setal formula of legs 1–4 (based on Shiino, 1955) as follows:

	leg 1		*leg 2*		*leg 3*		*leg 4*	
	exp.	end.	exp.	end.	exp.	end.	exp.	end.
seg. 1	I:0	0:0	I:1	0:1	I:1	0:1	I:1	0:1
seg. 2	IV:3	3	I:1	0:2	I:1	0:2	I:1	5
seg. 3			III:5	6	III:4	4	III:4	

It is interesting to note that the egg strings remain recurved and hidden beneath the genital segment as in some other members of group II (*Demoleus latus* and *Dinemoura discrepans*).

The male is unknown.

Comparative External Morphology and Taxonomic Relationships Within the Family Pandaridae

It seems appropriate to examine the family Pandaridae as a group and discuss the taxonomic features on a comparative basis. During the course of the study, it became apparent that certain features were quite stable, while others showed variations that should be pointed out. In some cases these variations can be explained reasonably on the basis of the ecology of the parasite.

Body form: The body of the adult is composed of a cephalon (head and first thoracic segment fused together), 3 free thoracic segments (nos. 2–4), a genital segment (thoracic segments 5 and 6 fused), and an abdomen (of 1 or 2 segments) that bears 2 caudal rami. In gen-

eral, the body of the female is more compact than that of the male. The thoracic segments tend to be more broadly joined to each other, making the females less flexible and adapted for a more sedentary existence. The male is not modified in this way and is more mobile than the female (compare figs. 1 and 16).

Cephalon: The cephalon is usually rounded in both sexes and concave on the ventral surface. This configuration is quite stable and found in most caligoid copepods. This is an obvious modification to aid in attaching to the host, the cephalon forming a sucking disc. The lateral borders usually bear a membrane. This thin flexible membrane further enhances the holding ability of the cephalon.

Thoracic segments: In all cases in both sexes segment 1 is fused to the head and segments 2–4 are free. The thoracic segments of the female may bear dorsal plates in one of two arrangements, plates present on segments 2–4 as in *Pandarus*, *Pseudopandarus*, *Gangliopus*, *Phyllothereus*, *Perissopus*, and *Pannosus*, or plates present on segment 4 only as in *Echthrogaleus*, *Demoleus*, *Pagina*, *Dinemoura*, *Nesippus*, and *Paranesippus*. This feature separates the females easily into 2 distinct groups.

Genital segment: The genital segment in both sexes is well formed. In the female the genital segment may comprise more than one-half of the total length (as in *Pseudopandarus*) and in all cases is at least one-third of the total length of the copepod.

Abdomen: The abdomen of the female is 1-segmented in all genera except *Pagina* and *Dinemoura*. The segments of the abdomen bear dorsal plates except in the genera *Nesippus* and *Paranesippus*. The abdomen may be joined to the genital segment ventrally or terminally. In the male the abdomen is of 2 segments except in the genus *Nesippus*, in which there is only 1. None of the males have dorsal abdominal plates.

Caudal rami: There is a great deal of variation in the form of the rami in the females of this family. In the genus *Pandarus* the rami are attached laterally to the abdomen and are often strongly sclerotized and elongated, terminating in a point (see figs. 2, 28, 35, 110). In *Pandarus bicolor* (see fig. 101) the rami are not elongated but are attached laterally to the abdomen.

It is interesting to note that the 2 genera *Phyllothereus* and *Gangliopus*, which are found only on gill filaments of the hosts, show a great reduction in adhesion pads. *Dinemoura ferox* and *D. discrepans* also have no adhesion pads. Both these species are found on the body surface, and the loss of pads is unexplained in these cases.

First antenna: In both sexes of all members of this family the first antenna is 2-segmented. The first segment bears terminally a number of spines that are often covered with spinules or hairs.

The last segment bears a smaller number of naked setae in all cases. This appendage is not of great taxonomic importance on the generic or specific level.

Second antenna: This appendage is well developed in all members and serves as a principal means of attachment. The tip is always in the form of a claw and this reaches its greatest development in the females of the genera *Phyllothereus* and *Gangliopus* (see fig. 127). These genera, as previously pointed out, show a reduction in adhesion pads and also are the only pandarids found routinely on the gill filaments. In view of this location on the host, adhesion pads would not be as

TABLE 2.—Arrangement of female cephalic adhesion pads in genera of the family Pandaridae (+=present, −=absent)

Genus	Cephalic Adhesion Pads				
	A1	A2	base of Mxpd	between Mxpd	distal corner of cephalon
Pandarus	+	+	+	−	+
Pseudopandarus	+	+	+	−	+
Perissopus	+	+	+	−	−
Paranesippus	+	+	+	−	−
Pannosus	+	+	+	−	−
Nesippus	hooklike	+	+	−	−
Dinemoura (part)	double	+	+	−	−
Demoleus	+	+	+	+	−
Pagina	+	−	−	−	−
Echthrogaleus	+	+	hooklike	−	−
Phyllothereus	−	−	−	−	−
Dinemoura (part)	−	−	−	−	−
Gangliopus	−	−	+	−	−

useful whereas a well-developed claw to envelope the gill filament would be. The terminal claw always bears 2 setae.

Mouth tube: The mouth tube is composed of the labrum and labium, forming a conelike structure, within which is housed the stylus of the mandible. The tip of the labium is fringed (see figs. 6, 167, 251). The labium extends beyond the tip of the labrum. The labrum bears 2 accessory spinelike structures at its tip (see fig. 251).

Mandible: The mandible is composed of a basal segment located near the base of the mouth tube and a long stylet projecting within the tube. The tip of the stylet is armed with 10–12 teeth. This appendage is of little taxonomic value and shows little variation from species to species in both sexes.

First maxilla: This appendage is attached laterally to the base of

the mandible (see fig. 6) and is composed of a basal segment bearing a group of 3 short setae anteriorly and a posteriorly directed process. Within the family this appendage takes 2 basic forms. In members of group I, plus *Nesippus*, the first maxilla is represented by a basal segment fused to the cephalon along its entire length and bearing a group of 3 short setae and a more prominent spine, generally directed posteriorly. The appendage does not appear to have much mobility (see figs. 6, 75, 113, 128, 168). In the genera *Pagina*, *Echthrogaleus*, *Dinemoura*, and *Demoleus* (all of group II), the first maxilla is attached to the cephalon at the anterior margin of the basal segment and gives the appearance of greater freedom of movement (see figs. 224, 253, 269).

Second maxilla: The second maxilla in all species bears a clawlike tip that usually bears rows of fringe or spinules. Group I can be separated from group II by the nature of this appendage. In group I there are 2 prominent spines near the base of the claw (see figs. 9, 76, 129, 149, 169). In group II the smaller spine is replaced by a patch of setules or spinules (see figs. 204, 225, 254, 282). This distinction is present in both sexes.

Maxilliped: The maxilliped is in all species a strongly developed appendage. It undoubtedly aids in holding the copepod to the host or is used by the male to hold the female during copulation. It is interesting to note that, in group I, 3 genera found on the body surface of the host possess a maxilliped with a spatulate tip on the claw (*Pandarus*, *Pseudopandarus*, and *Pannosus*). This modification would seem to enable the parasite to grip the denticles of the host better. The remaining genus (*Perissopus*) of group I found on the body surface of the host attaches by cementing the maxilliped to the host. The 2 genera of group I found on the gills have pointed claws on the maxilliped. All members of group II have sharply pointed or rounded tips on the claw of the maxilliped. None are spatulate.

Leg 1: This appendage is relatively stable in pandarid copepods, but 2 genera can be separated from the rest of the family on the basis of the endopod. In *Pandarus* the endopod is 1-segmented. In all other known members of the family the endopod is 2-segmented. In *Perissopus* the endopod is unarmed. In all other members of the family the endopod bears 3 setae.

Leg 2: In group I the exopod of all species is 2-segmented. In group II all genera have 3-segmented exopods except *Demoleus* and *Nessipus*, which have only 2.

Leg 3: The situation regarding this appendage is like that of leg 2. All members of group II (except *Demoleus*, with only 2) have 3-segmented exopods. Copepods of group I have a 2-segmented exopod except *Perissopus*, which has only 1.

Leg 4: In many genera of both groups this leg in the female is lamelliform (*Pandareus*, *Phyllotherus*, *Echthrogaleus*, and *Dinemoura*). The females of these genera can be separated from other female members of the family on this basis alone. In the male the leg is not modified and is of more usual form.

Leg 5: This leg is reduced in both sexes and is represented by a group of 2–4 setae. This appendage is not useful in separating members of the family.

Leg 6: This leg is incorporated in the female into the area of spermatophore attachment and is more obvious in group II species (see figs. 209, 284). In the male this leg is represented by 2 setae located near the union of the abdomen and genital segment in all members of the family in which the male is known.

It should be noted here that certain observations were made regarding the determination of adult males. It was noted (see page 14) that often, in collections, 2 sizes of males showing spermatophores were present. A closer examination indicated that the larger was more mature than the smaller (based on relative development of the spermatophores). It was obvious that in a collection where only the smaller ones were present that these might be erroneously considered as mature. I found that in the larger forms the pad of the second antenna was only about one-half the size of the pad of the first antenna. In the smaller forms they are of about equal size. The opinion is therefore presented that this difference may be a method of determining sexual maturity of the male since the spermatophore is seen in earlier stages and is not a dependable criterion. It was observed that in mature males of other species of *Pandarus* this reduction of the pad of the second antenna was also present (see figs. 59, 60).

A List of Sharks Examined with the Pandarid Copepods Recovered from Them

(Number in parenthesis indicates collections made)

Hexanchus species
- *Demoleus paradoxus* (1)

Isurus oxyrhynchus
- *Pandarus smithii* (3)
- *Dinemoura producta* (1)
- *Dinemoura latifolia* (3)
- *Echthrogaleus denticalatus* (3)

Lamna nasus
- *Pandarus floridanus* (1)
- *Echthrogaleus coleoptratus* (1)

Lamna ditropis
- *Echtrogaleus coleoptratus* (1)

Carcharodon carcharias
- *Pandarus smithii* (1)
- *Pandarus floridanus* (4)
- *Dinemoura producta* (1)

Cetorhinus maximus
- *Dinemoura producta* (1)

Alopias superciliosus
- *Dinemoura discrepans* (2)
- *Pagina tunica* (3)

Alopias pelagicus
- *Echthrogaleus denticulatus* (1)

Alopias vulpinus
- *Pandarus smithii* (2)
- *Dinemoura discrepans* (2)
- *Echthrogaleus denticulatus* (3)

Ginglymostomum cirratum
- *Nesippus orientalis* (1)

Mustelus species
- *Perissopus dentatus* (1)

Carcharinus milberti
- *Perissopus dentatus* (1)
- *Nesippus orientalis* (1)
- *Nesippus crypturus* (1)

Carcharinus maculipinnus
- *Perissopus dentatus* (1)
- *Pandarus sinuatus* (2)
- *Pandarus carcharini* (2)
- *Nesippus orientalis* (5)
- *Nesippus crypturus* (1)

Carcharinus leucas
- *Perissopus dentatus* (1)
- *Pandarus sinuatus* (2)
- *Pandarus carcharini* (2)
- *Nesippus orientalis* (5)
- *Nesippus crypturus* (1)

Carcharinus gangeticus
- *Pandarus carcharini* (1)

Carcharinus sorrah
- *Pandarus carcharini* (1)

Carcharinus limbatus
- *Pandarus smithii* (1)
- *Pandarus carcharini* (1)

Carcharinus obesus
- *Pseudopandarus longus* (1)

Carcharinus malpeloensis
- *Pandarus cranchii* (1)
- *Pandarus smithii* (1)
- *Pandarus katoi* (5)

Carcharinus galapagensis
- *Pandarus cranchii* (1)
- *Pandarus smithii* (1)
- *Nesippus crypturus* (1)

Carcharinus azureus
- *Pandarus smithii* (2)
- *Pandarus katoi* (2)

Carcharinus platyrhynchus
- *Pandarus katoi* (1)

Pterolamiops longimanus
- *Pandarus cranchii* (27)

Eulamia floridanus
- *Pandarus cranchii* (12)
- *Pandarus smithii* (4)
- *Echthrogaleus denticulatus* (1)

Eulamia falciformis
- *Pandarus cranchii* (2)
- *Pandarus smithii* (2)

Eulamia obscura
- *Pandarus cranchii* (2)

Hypoprion signatus
- *Pandarus smithii* (1)

Prionace glauca
- *Pandarus satyrus* (35)
- *Echthrogaleus coleoptratus* (30)
- *Phyllothereus cornutus* (8)
- *Gangliopus pyriformis* (4)
- *Dinemoura producta* (1)

Galeocerdo cuvier
- *Pandarus cranchii* (2)
- *Nesippus tigris* (2)
- *Nesippus orientalis* (2)
- *Nesippus crypturus* (2)

Negaprion brevirostris
Pandarus sinuatus (1)
Galeorhinus species
Pandarus niger (1)
Pandarus carcharini (1)
Scoliodon palasorrah
Pseudopandarus gracilis (1)
Nesippus orientalis (1)
Nesippus crypturus (1)
Rhizoprionodon acutus
Pseudopandarus longus (1)
Sphyrna mokarran
Nesippus crypturus (1)
Sphyrna lewini
Nesippus orientalis (4)
Nesippus crypturus (4)
Sphyrna zygaenae
Pandarus cranchii (1)
Pandarus smithii (1)
Pandarus zygaenae (3)
Nesippus orientalis (1)
Squalus acutipinnus
Demoleus latus (1)
Squalus acanthias
Pandarus bicolor (1)
Rhynchobatus djeddensis
Nesippus nana (1)

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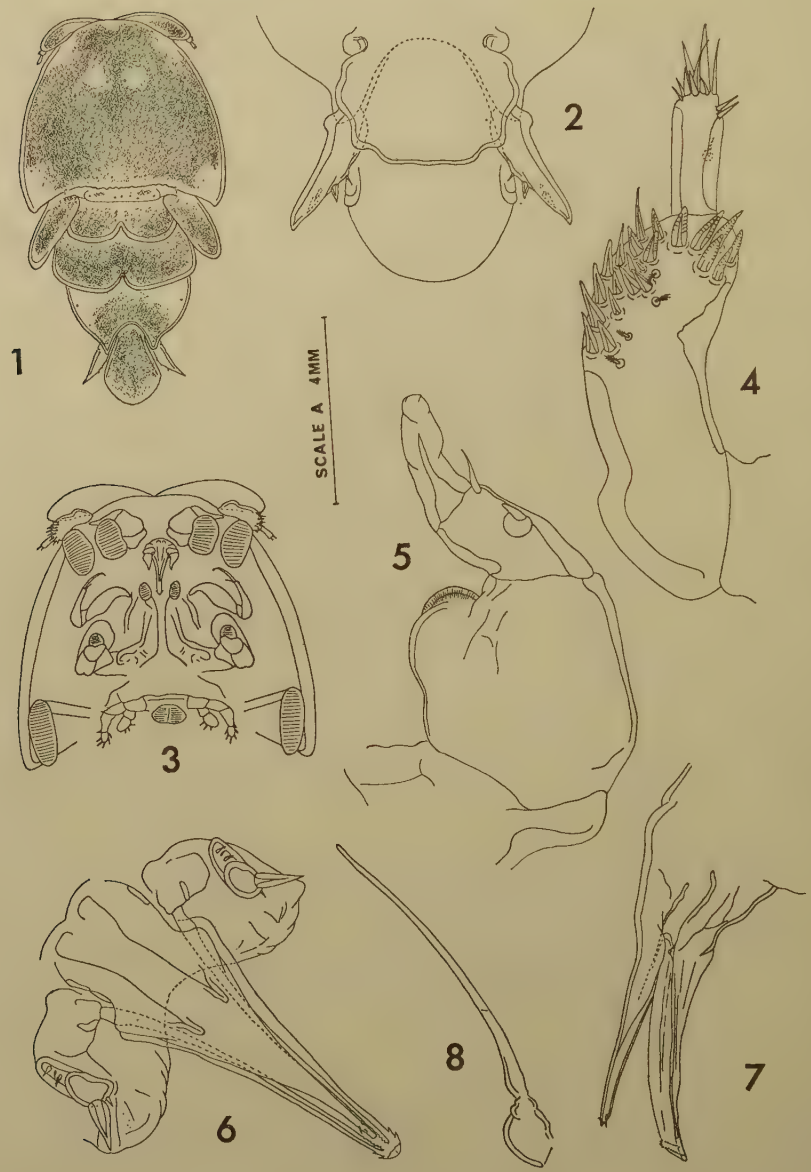
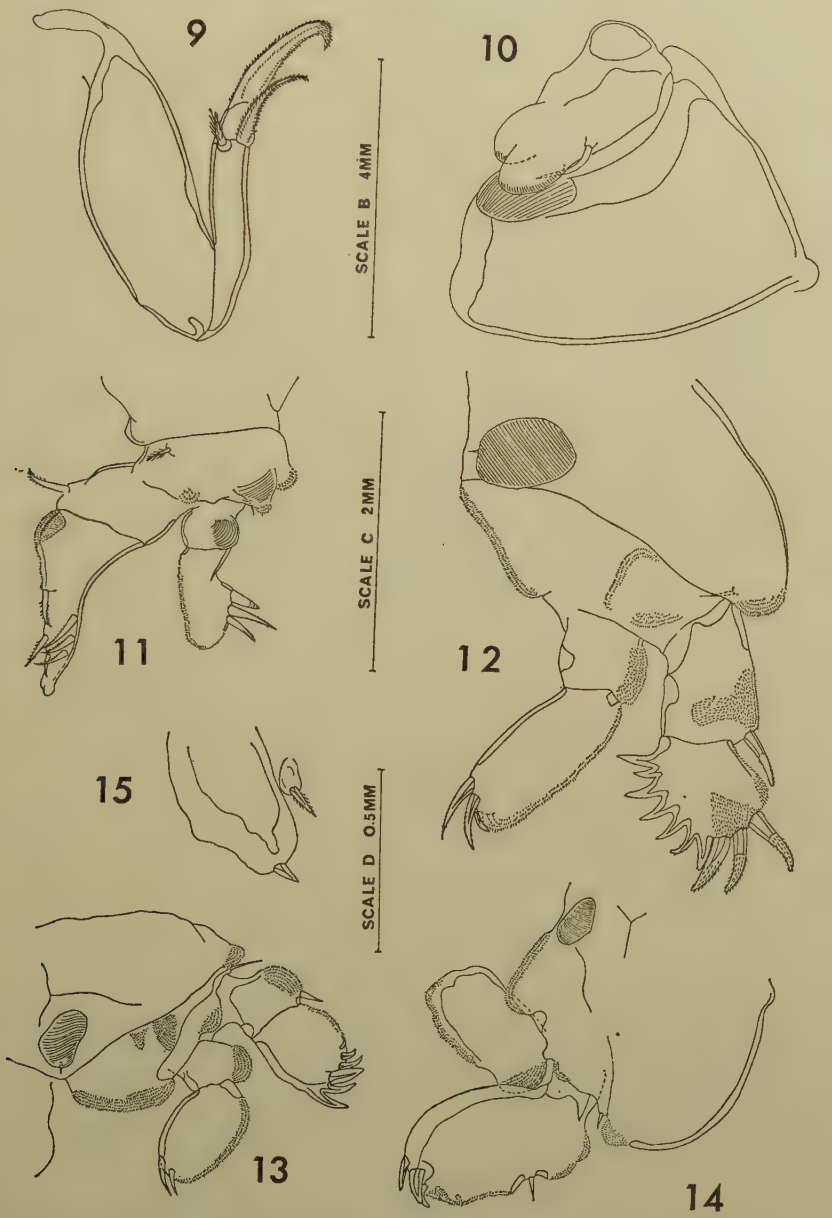
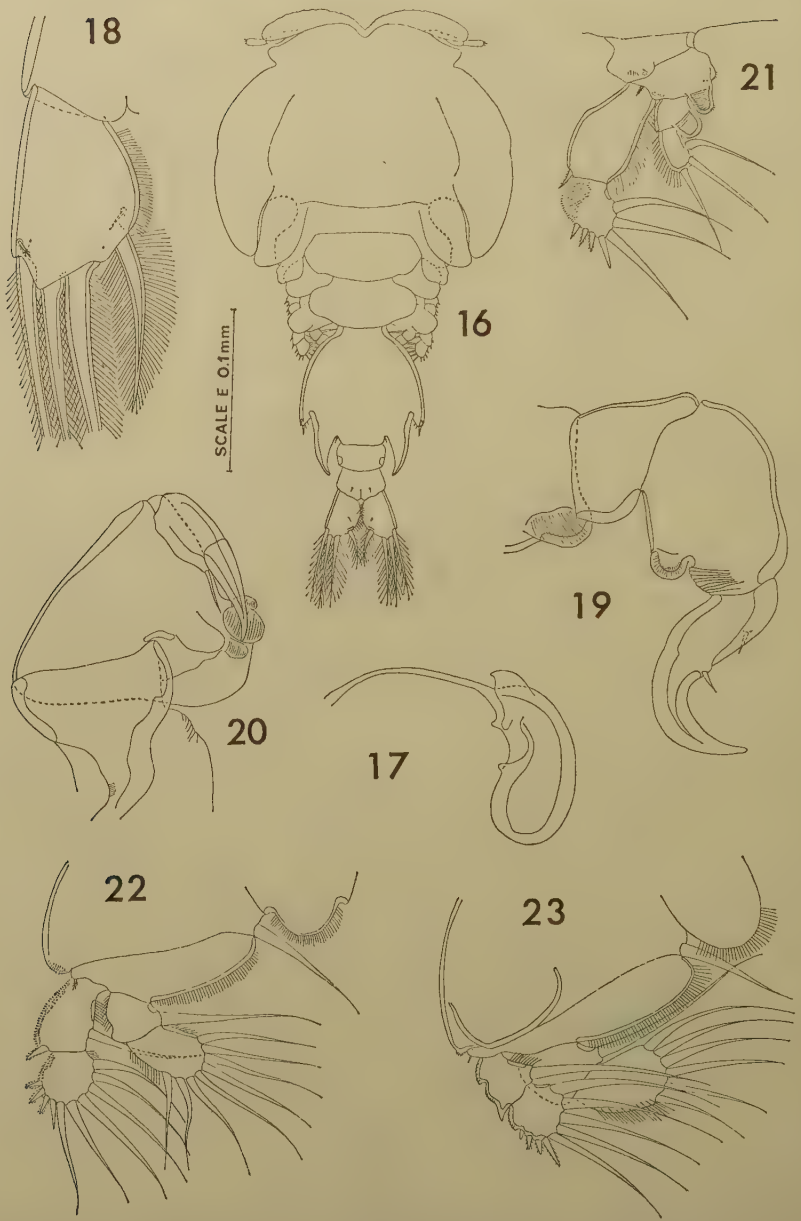


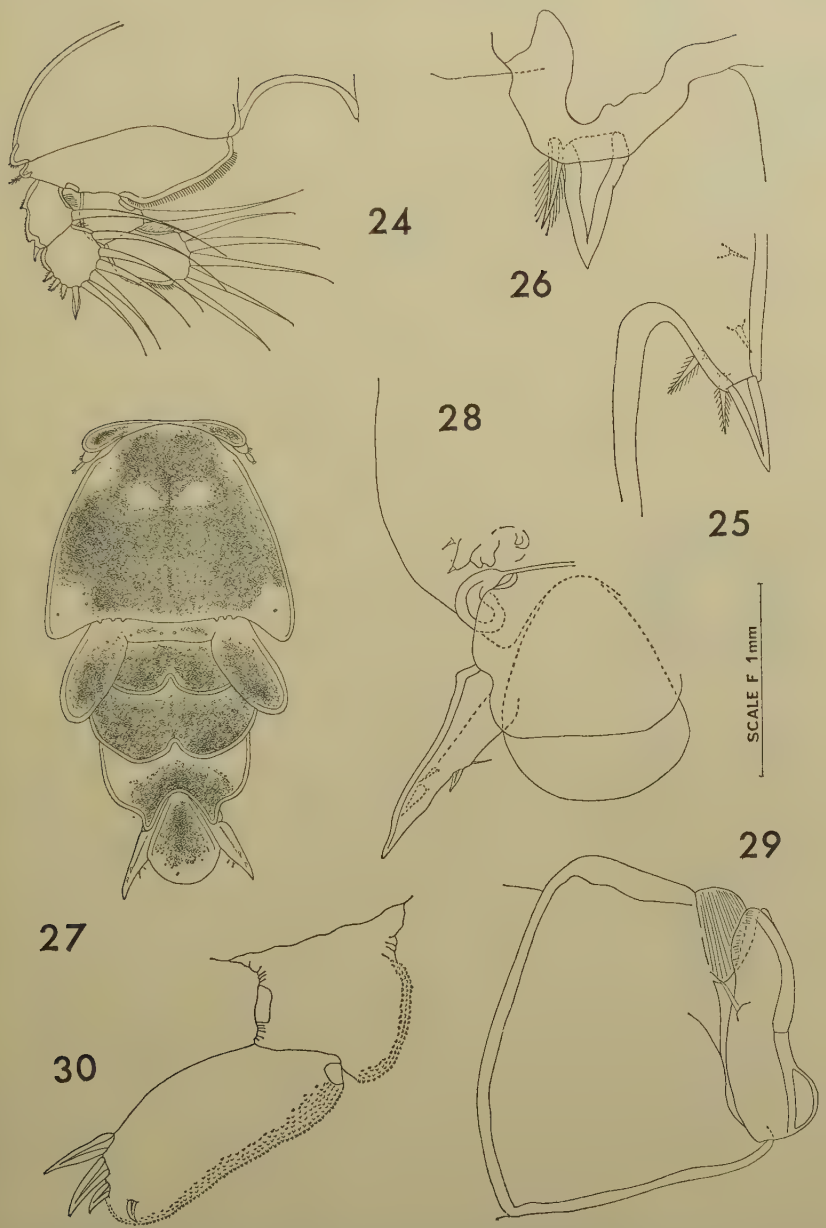
FIGURES 1–8.—*Pandarus satyrus*, female: 1, dorsal (A); 2, abdomen and caudal rami ventral (D); 3, oral area, ventral (B); 4, first antenna (G); 5, second antenna (G); 6, mouth tube and first maxilla (G); 7, mouth tube, lateral (G); 8, mandible (G).



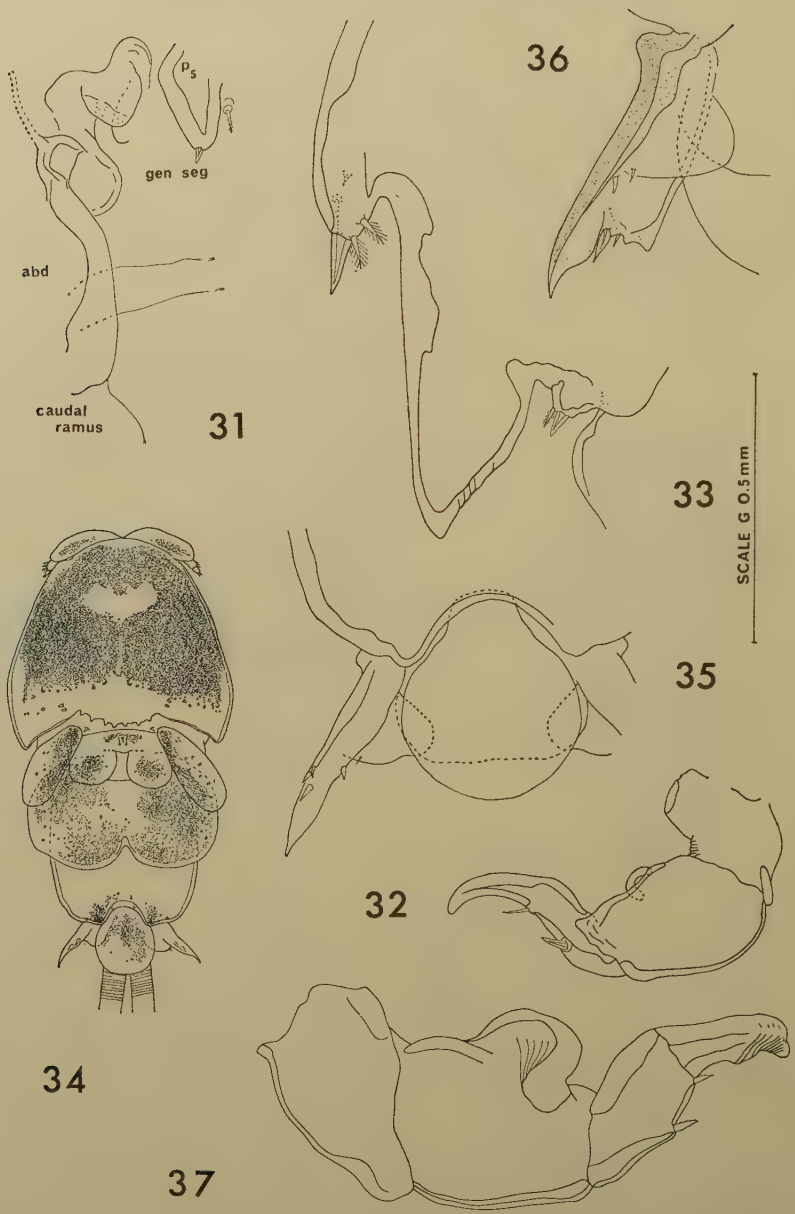
FIGURES 9–15.—*Pandarus satyrus*, female: 9, second maxilla (D); 10, maxilliped (D); 11, leg 1 (D); 12, leg 2 (D); 13, leg 3 (F); 14, leg 4 (F); 15, leg 5 (G).



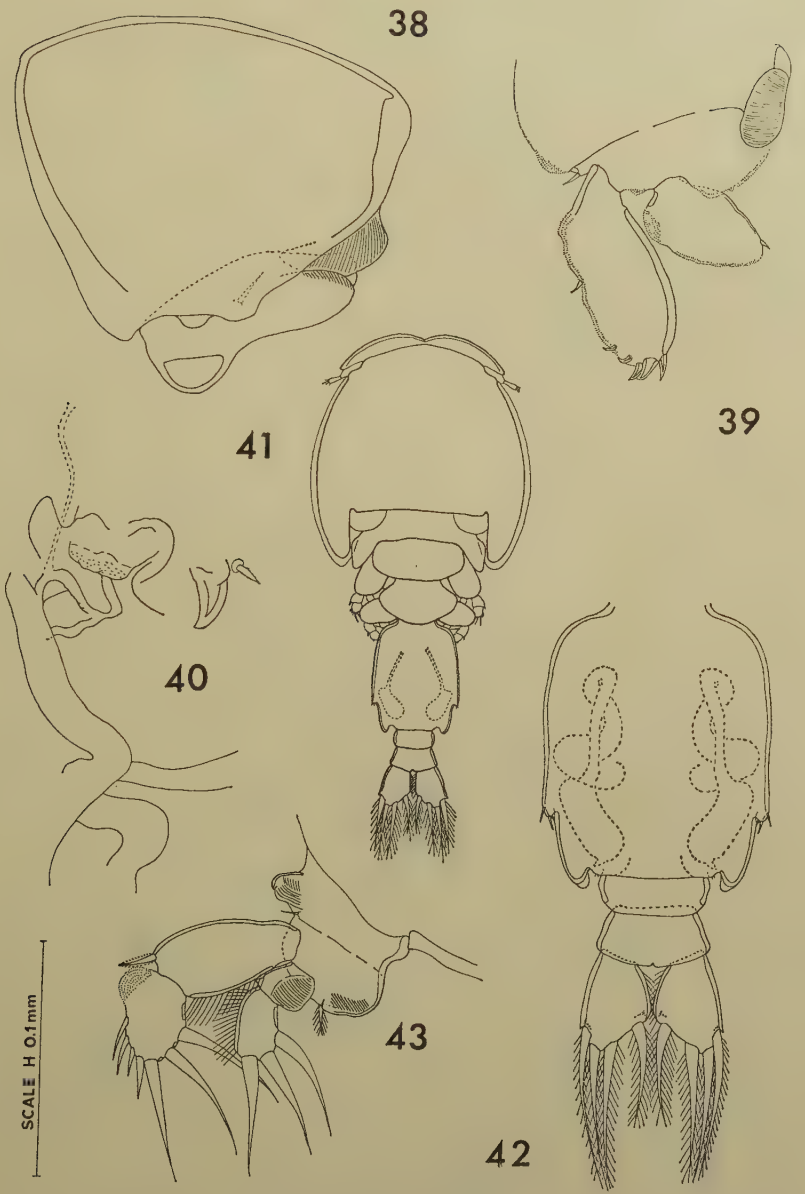
FIGURES 16–23.—*Pandarus satyrus*, male: 16, dorsal (A); 17, spermatophore (G); 18, caudal ramus (F); 19, second antenna (D); 20, maxilliped (F); 21, leg 1 (F); 22, leg 2 (F); 23, leg 3 (F).



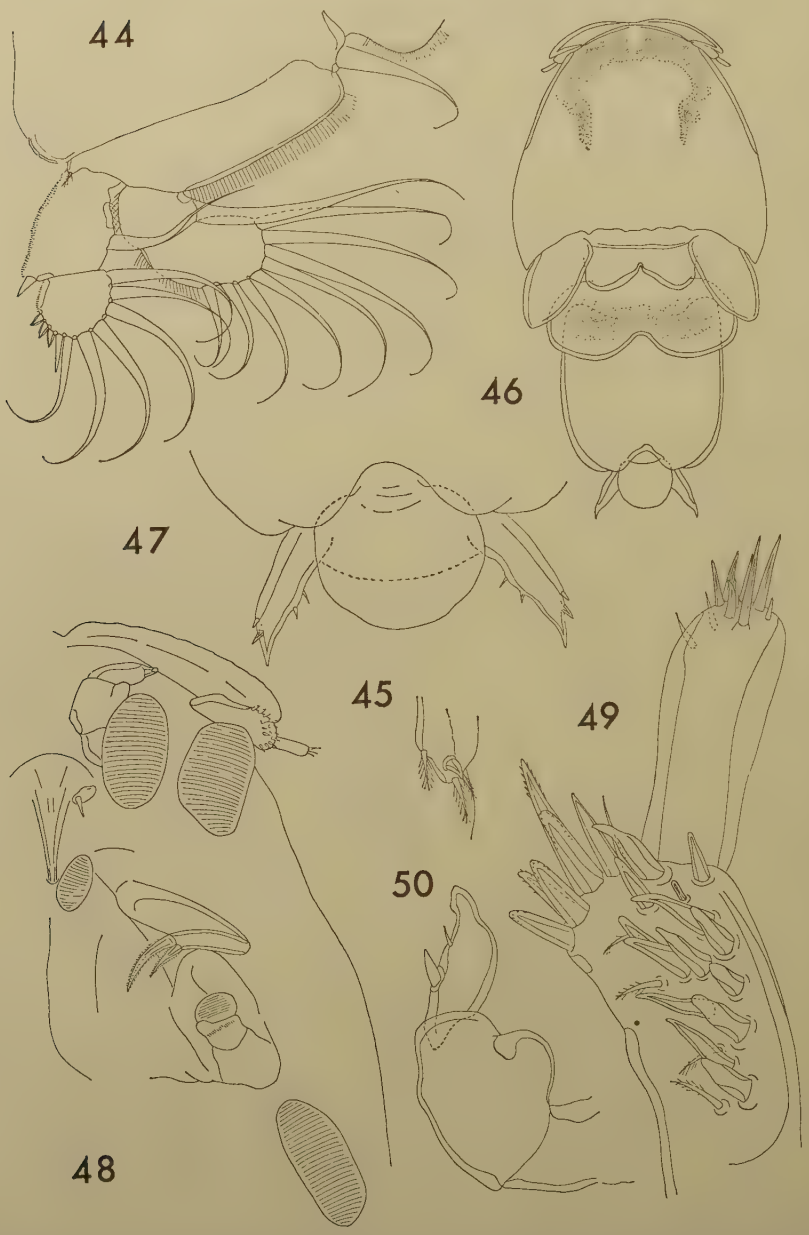
FIGURES 24–30.—*Pandarus satyrus*, male: 24, leg 4 (F); 25, leg 5 (G); 26 leg 6 (E). *P. cranchii*, female: 27, dorsal (A); 28, abdomen and caudal ramus (C); 29, maxilliped (D); 30, endopod of second leg (G).



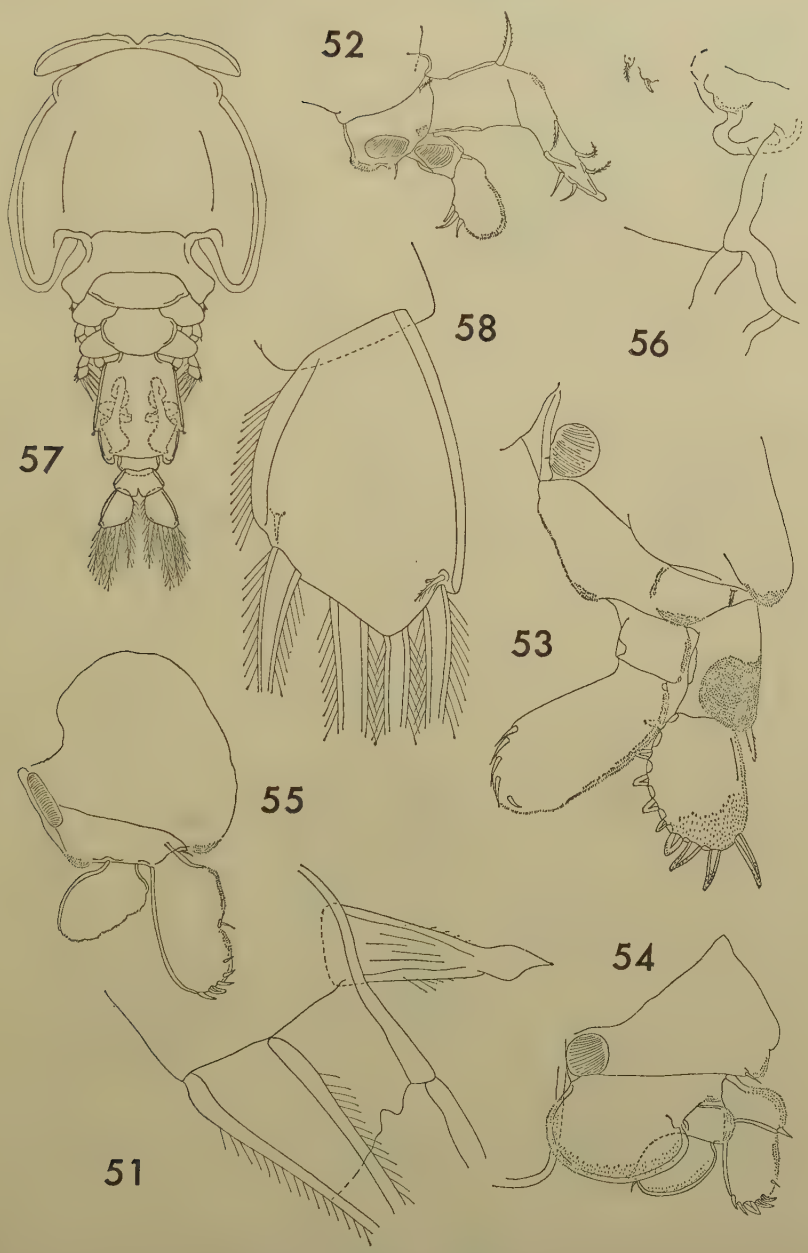
FIGURES 31–37.—*Pandarus cranchii*, female: 31, area of spermatohpore attachment (D); male: 32, second antenna (D); 33, posterior corner of genital segment (D). *P. smithii*, female: 34, dorsal (A); 35, abdomen and caudal ramus (D); 36, caudal ramus, ventrolateral (F); 37, second antenna (G).



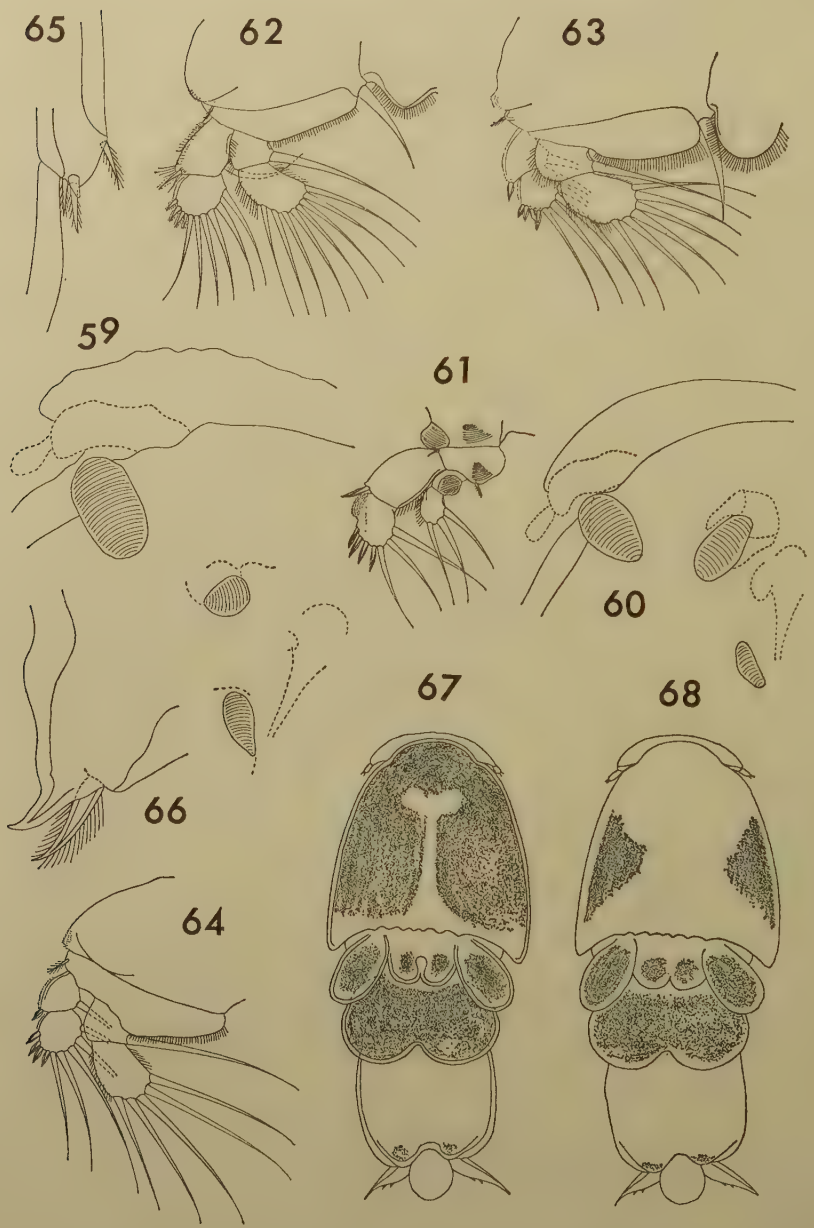
FIGURES 38–43.—*Pandarus smithii*, female: 38, maxilliped (D); 39, leg 4 (F); 40, area of spermatophore attachment (D); male: 41, dorsal (A); 42, genital segment and abdomen (C); 43, leg 1 (D).



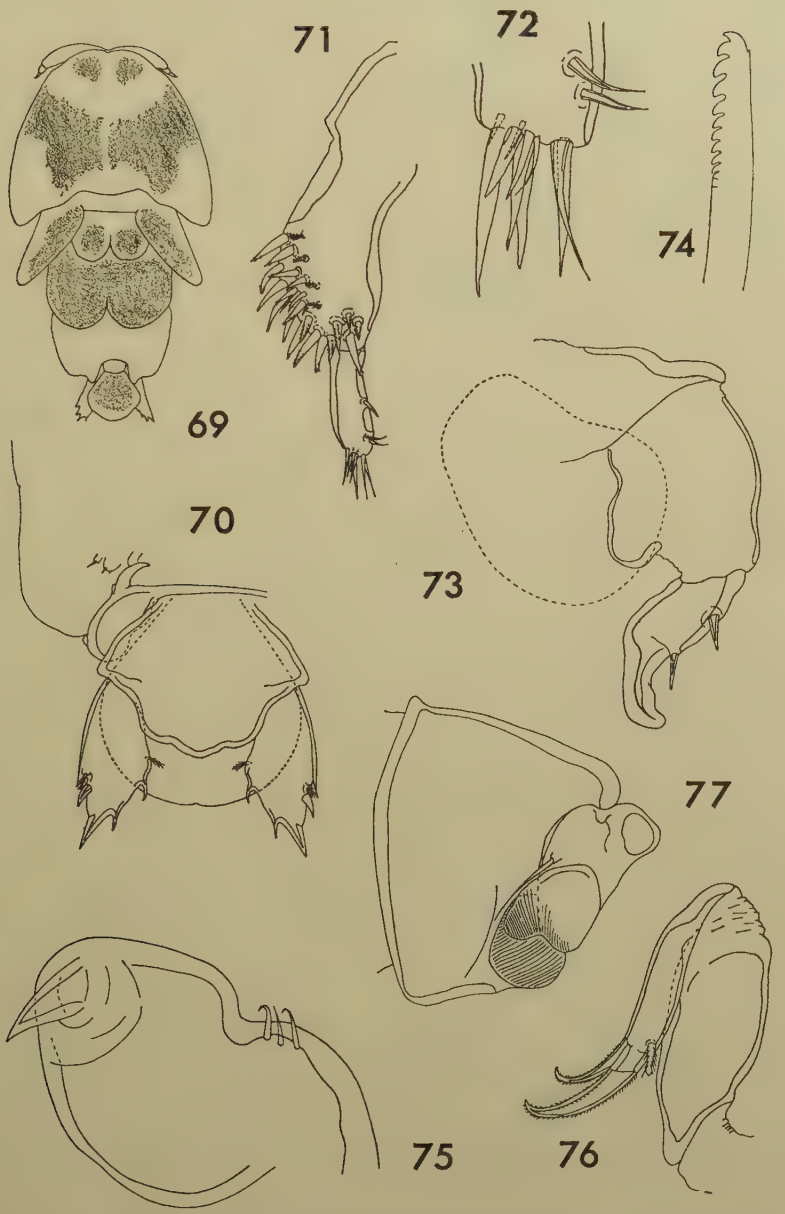
FIGURES 44–50.—*Pandarus smithii*, male: 44, leg 2 (D); 45, leg 5 (G). *P. floridanus*, new species, female: 46, dorsal (B); 47, dorsal abdominal plate and rami (F); 48, oral area (F); 49, first antenna (E); 50, second antenna (G).



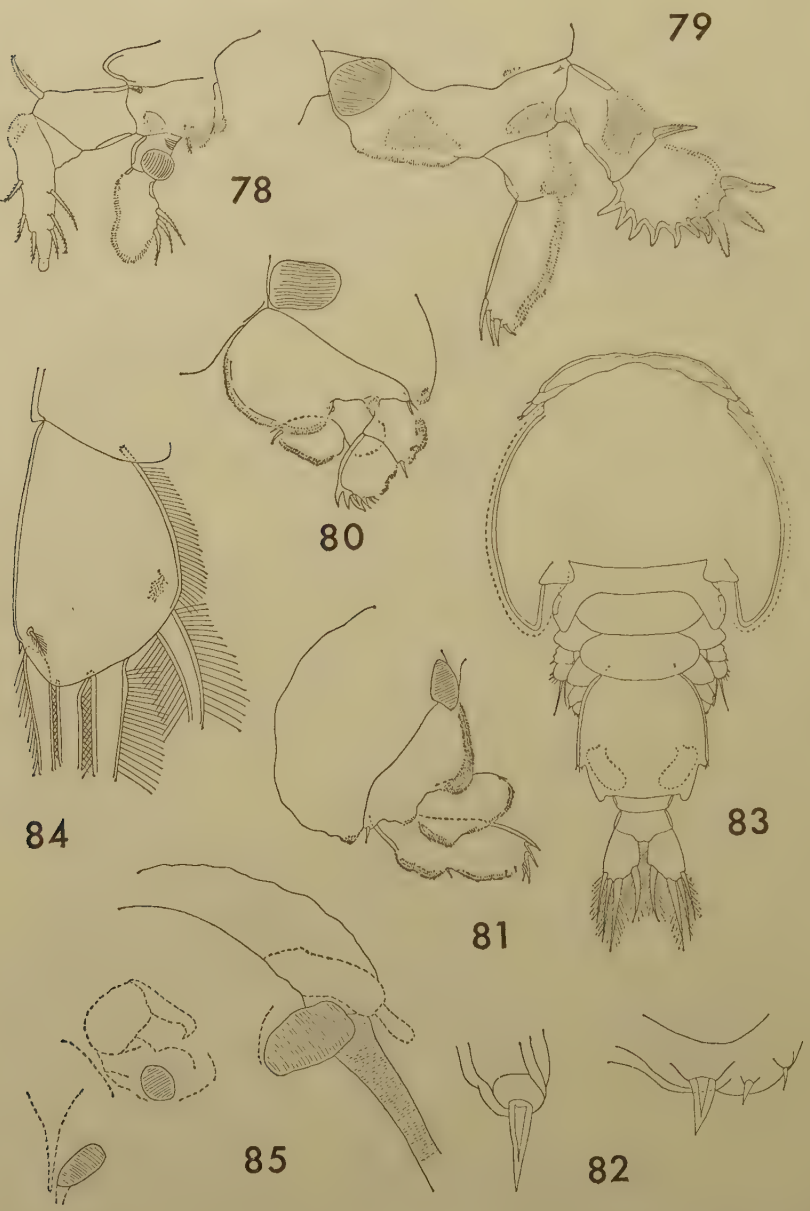
FIGURES 51–58.—*Pandarus floridanus*, new species, female: 51, subterminal spine on second maxilla (H); 52, leg 1 (D); 53, leg 2 (D); 54, leg 3 (F); 55, leg 4 (F); 56, area of spermatophore attachment (D). Male: 57, dorsal (C); 58, caudal ramus (G).



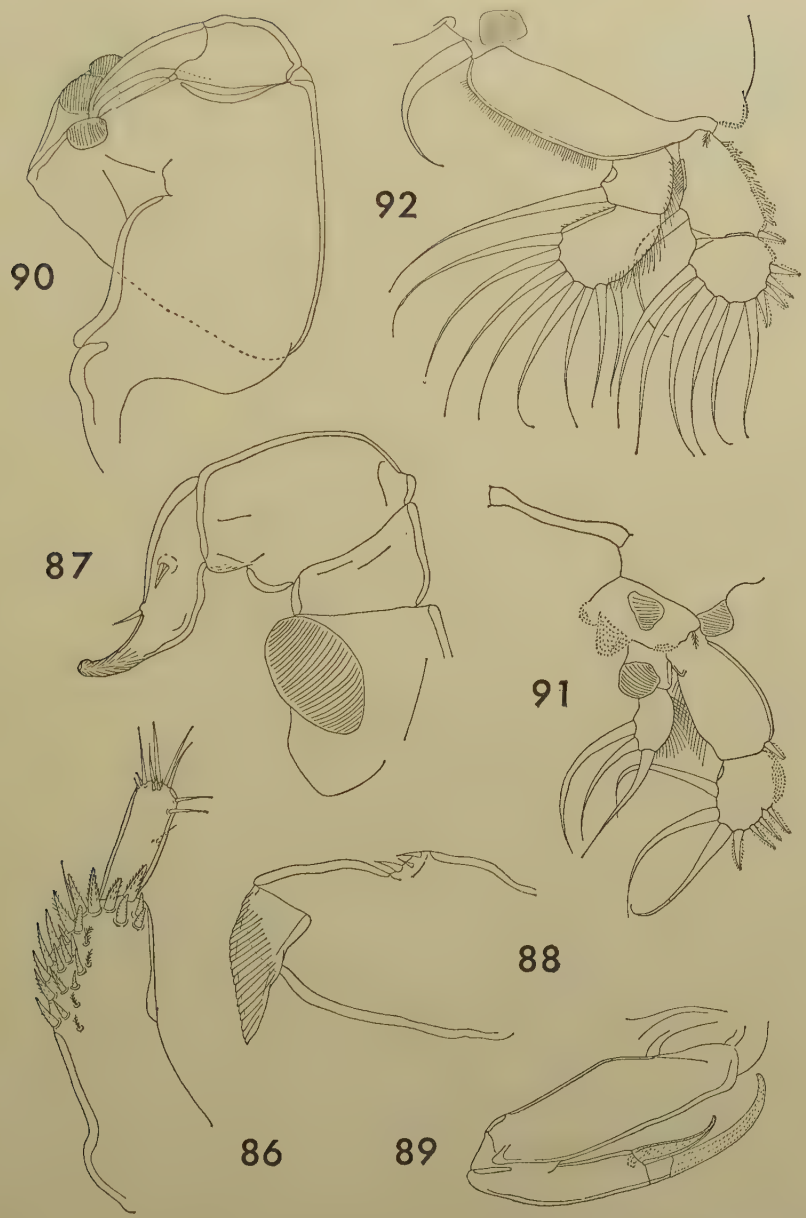
FIGURES 59–68.—*Pandarus floridanus*, new species, male: 59, adhesion pads, adult (F); 60, adhesion pads, young male (F); 61, leg 1 (F); 62, leg 2 (F); 63, leg 3 (F); 64, leg 4 (F); 65, leg 5 (G); 66, leg 6 (H). *P. sinuatus*, female: 67, dorsal, adult female (B); 68, dorsal, young female (B).



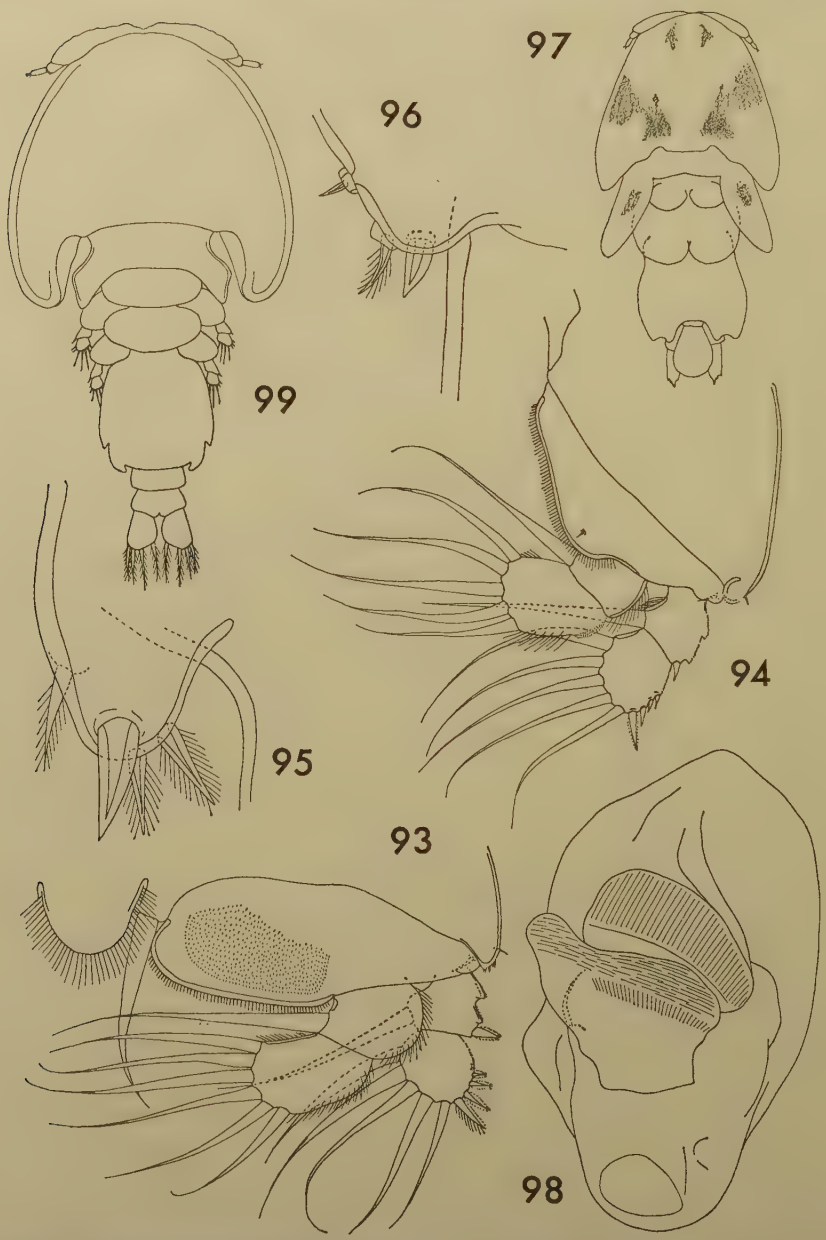
FIGURES 69–77.—*Pandarus katoi*, new species, female: 69, dorsal (A); 70, abdomen and caudal ramus (F); 71, first antenna (G); 72, detail of last segment of first antenna (H); 73, second antenna (G); 74, tip of mandible (?); 75, first maxilla (H); 76, second maxilla (D); 77, maxilliped (D).



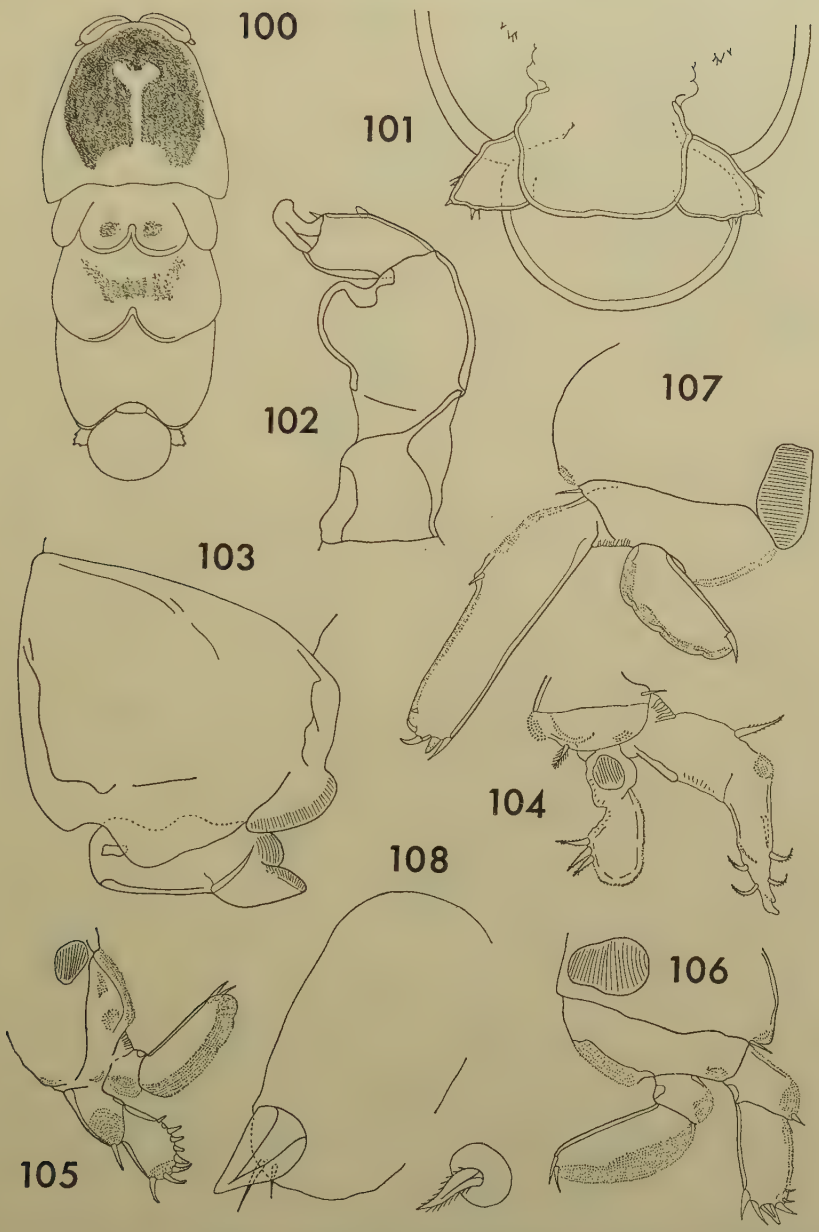
FIGURES 78–85.—*Pandarus katoi*, new species, female: 78, leg 1 (D); 79, leg 2 (D); 80, leg 3 (F); 81, leg 4 (F); 82, leg 5 (H). Male: 83, dorsal (B); 84, caudal ramus (D); 85, adhesion pads, oral area (F).



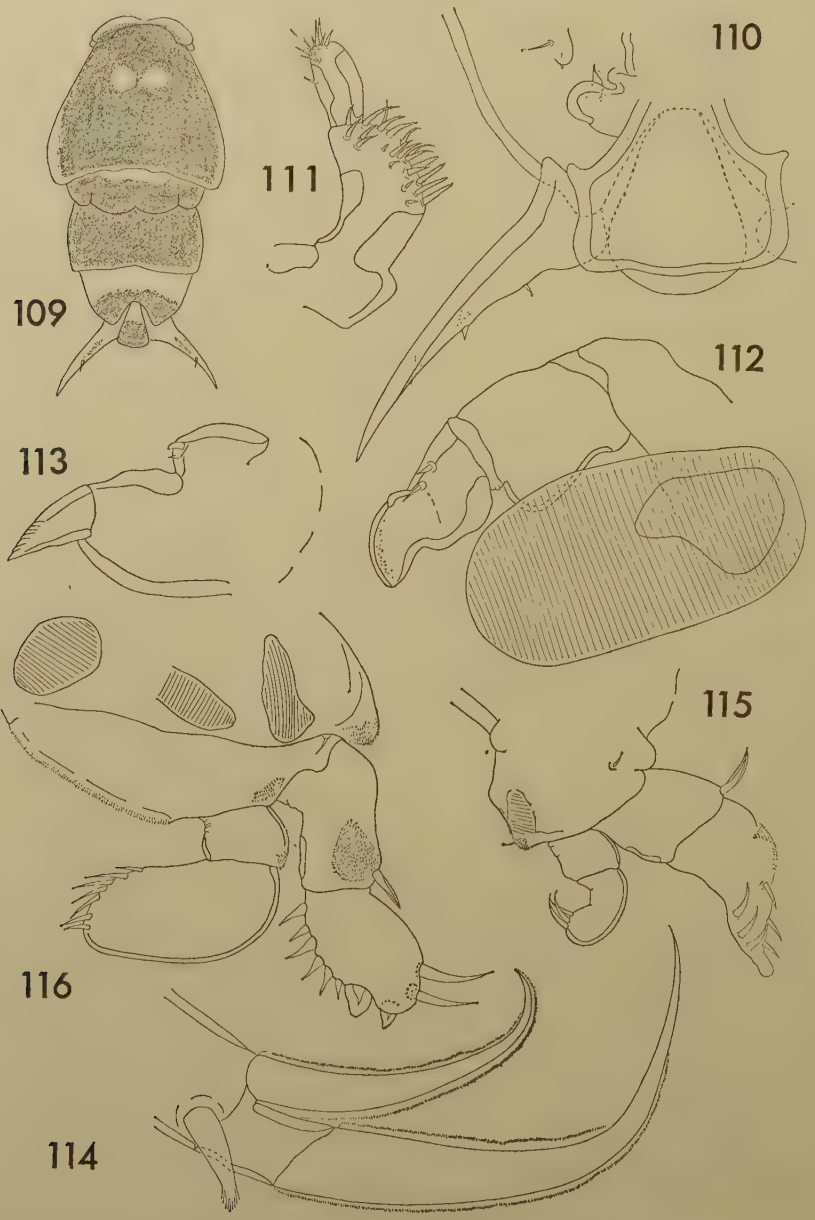
FIGURES 86–92.—*Pandarus katoi*, new species, male: 86, first antenna (G); 87, second antenna (G); 88, first maxilla (E); 89, second maxilla (D); 90, maxilliped (D); 91, leg 1 (D); 92, leg 2 (D).



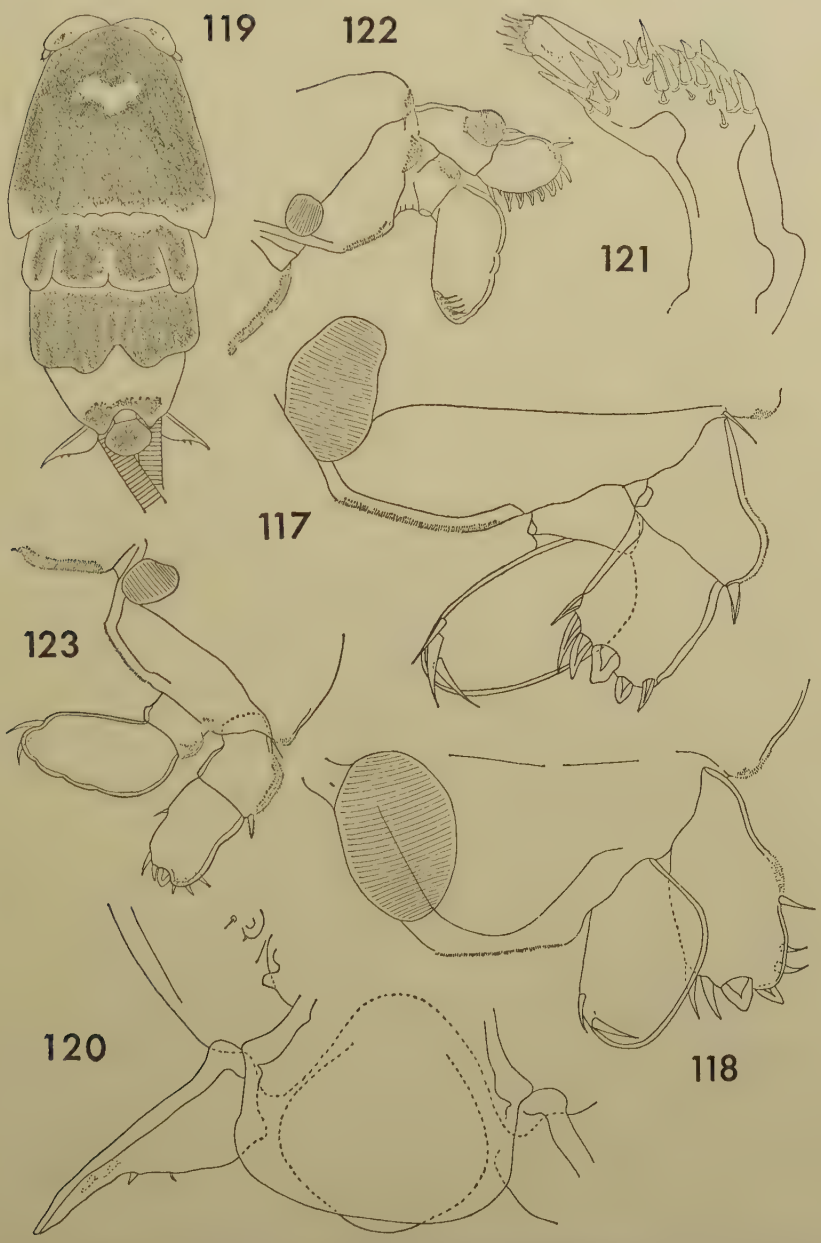
FIGURES 93–99.—*Pandarus kaloi*, new species, male: 93, leg 3 (D); 94, leg 4 (D); 95, leg 5 (E); 96, leg 6 (E). *P. zygaenae*, female: 97, dorsal (A); 98, maxilliped (G); male: 99, dorsal (B).



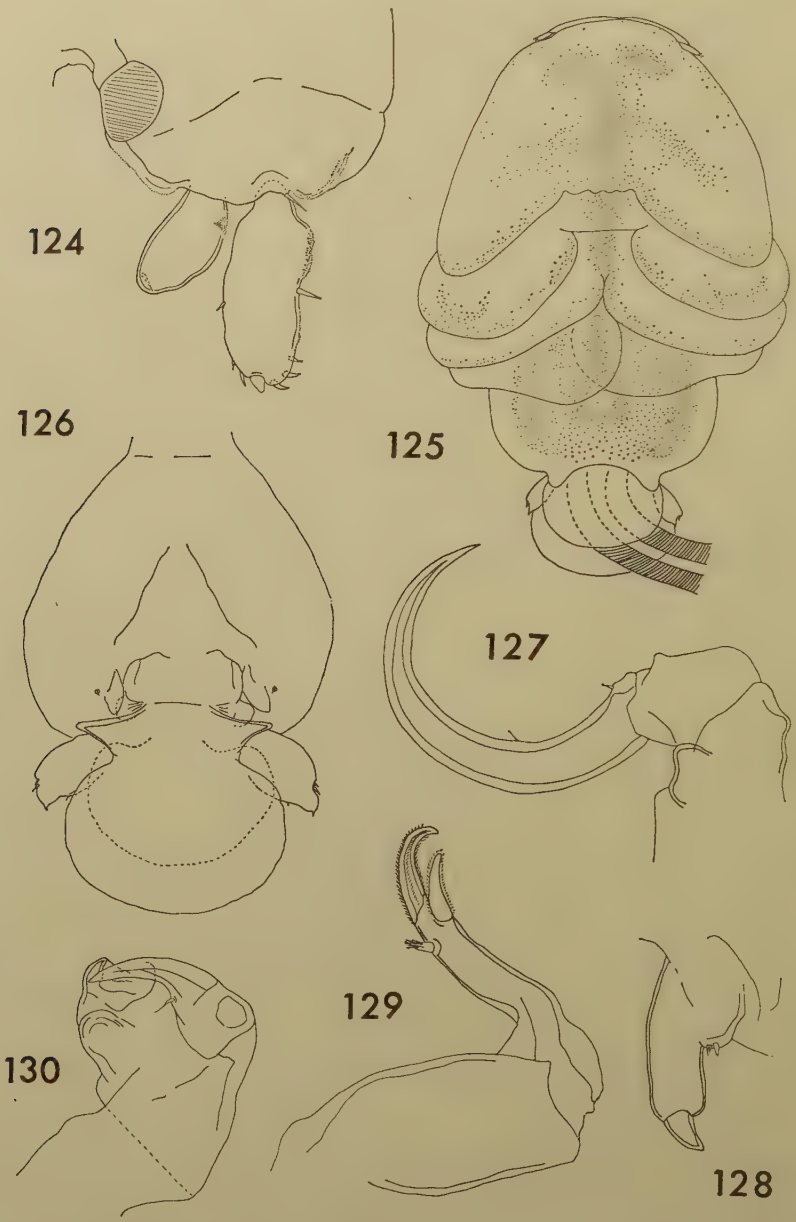
FIGURES 100–108.—*Pandarus bicolor*, female: 100, dorsal (A); 101, abdomen and caudal rami, ventral (C); 102, second antenna (G); 103, maxilliped (D); 104, leg 1 (D); 105, leg 2 (F); 106, leg 3 (G); 107, leg 4 (F); 108, leg 5 (H).



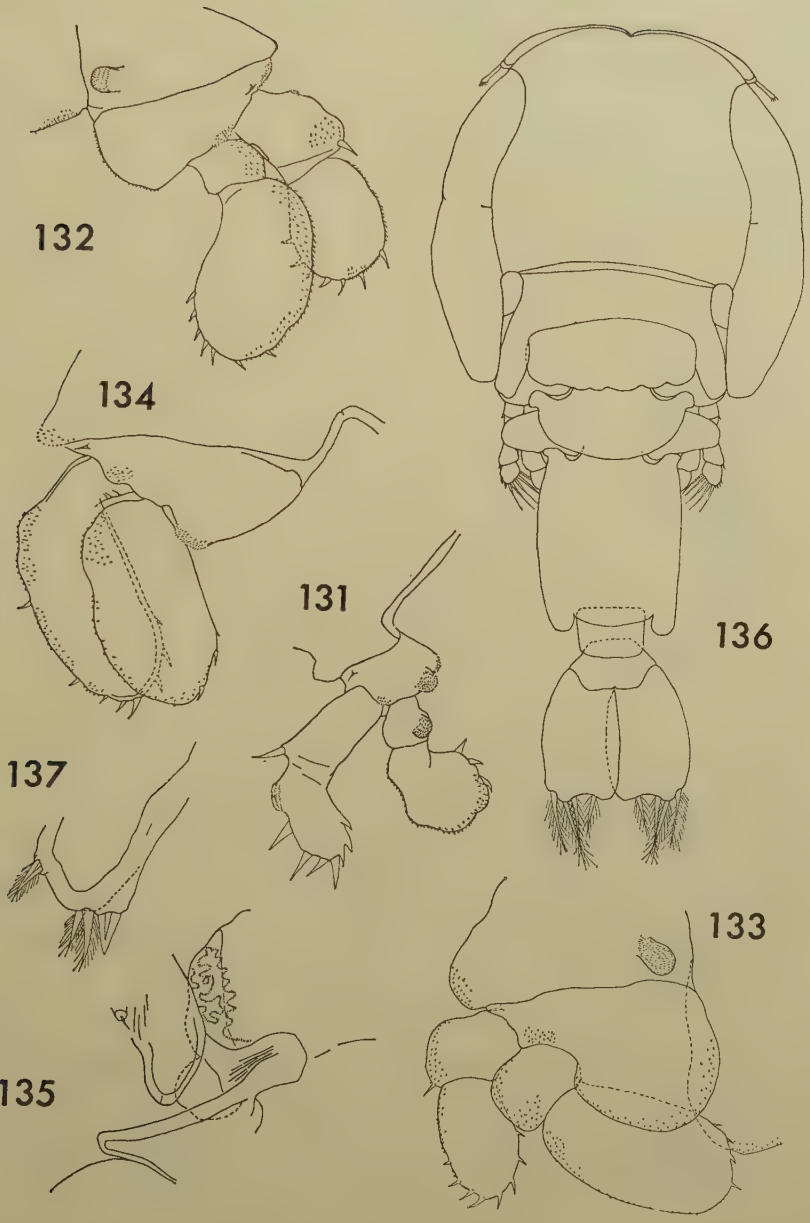
FIGURES 109–116.—*Pandarus niger*, female: 109, dorsal (A); 110, abdomen and caudal ramus, ventral (F); 111, first antenna (G); 112, second antenna (G); 113, first maxilla (E); 114, tip of second maxilla (E); 115, leg 1 (G); 116, leg 2 (G).



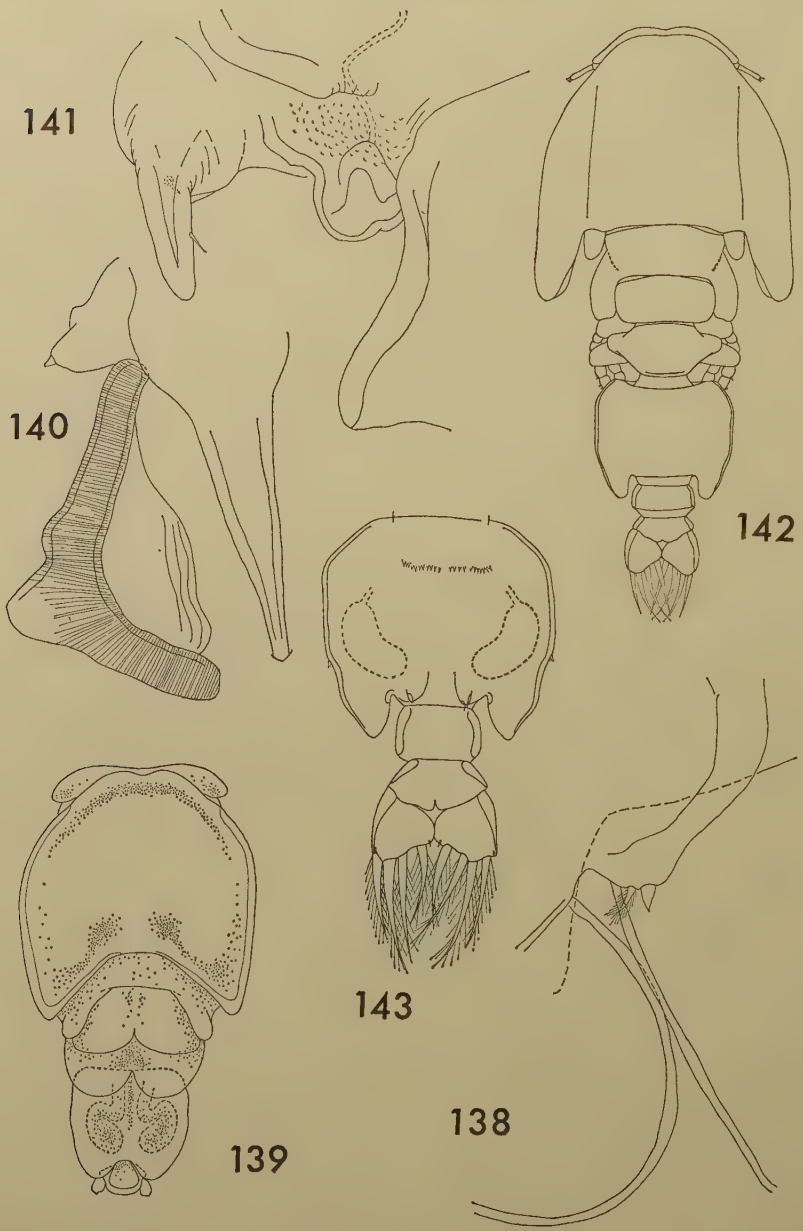
FIGURES 117–123.—*Pandarus niger*, female: 117, leg 3 (G); 118, leg 4 (G). *P. carcharini*, female: 119, dorsal (A); 120, abdomen and caudal ramus, ventral (F); 121, first antenna (G); 122, leg 2 (F); 123, leg 3 (F).



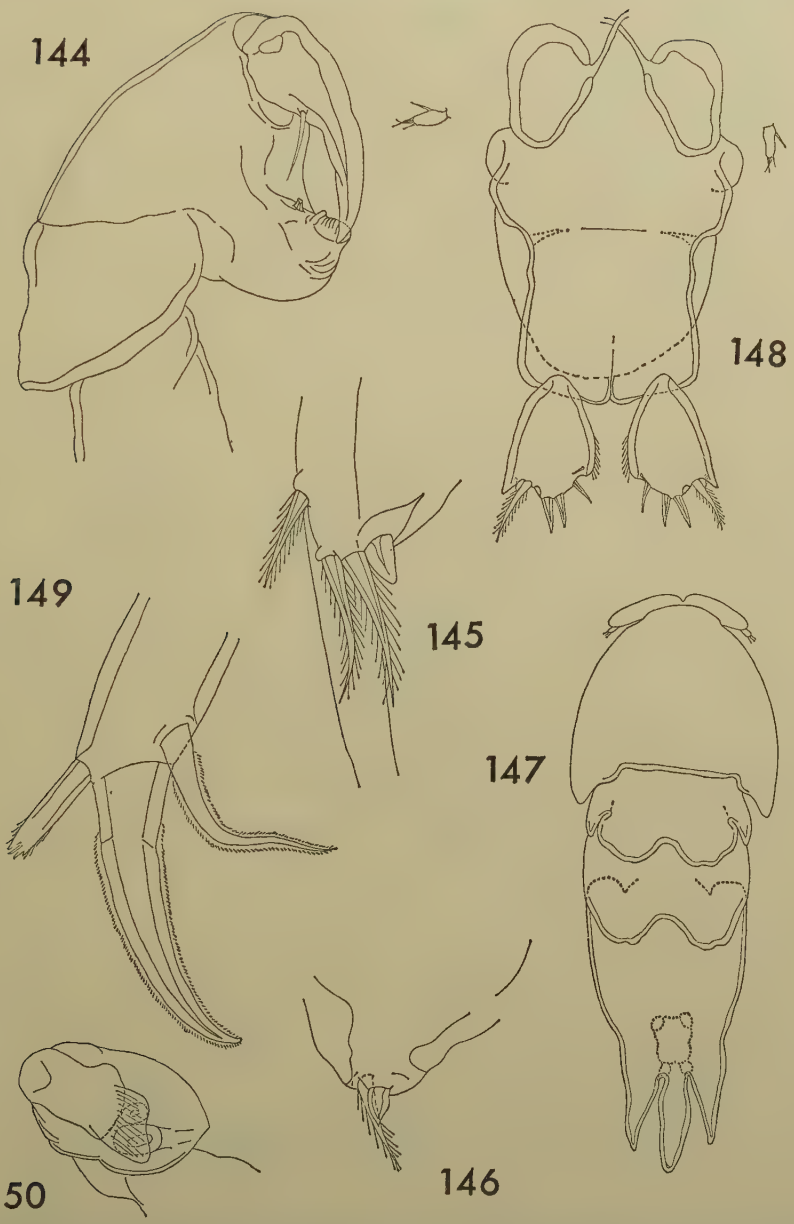
FIGURES 124–130.— *Pandarus carcharini*, female: 124, leg 4 (F). *Phyllothereus cornutus*, female: 125, dorsal (A); 126, genital segment, abdomen, and caudal rami, ventral (B); 127, second antenna (C); 128, first maxilla (G); 129, second maxilla (F); 130, maxilliped (F).



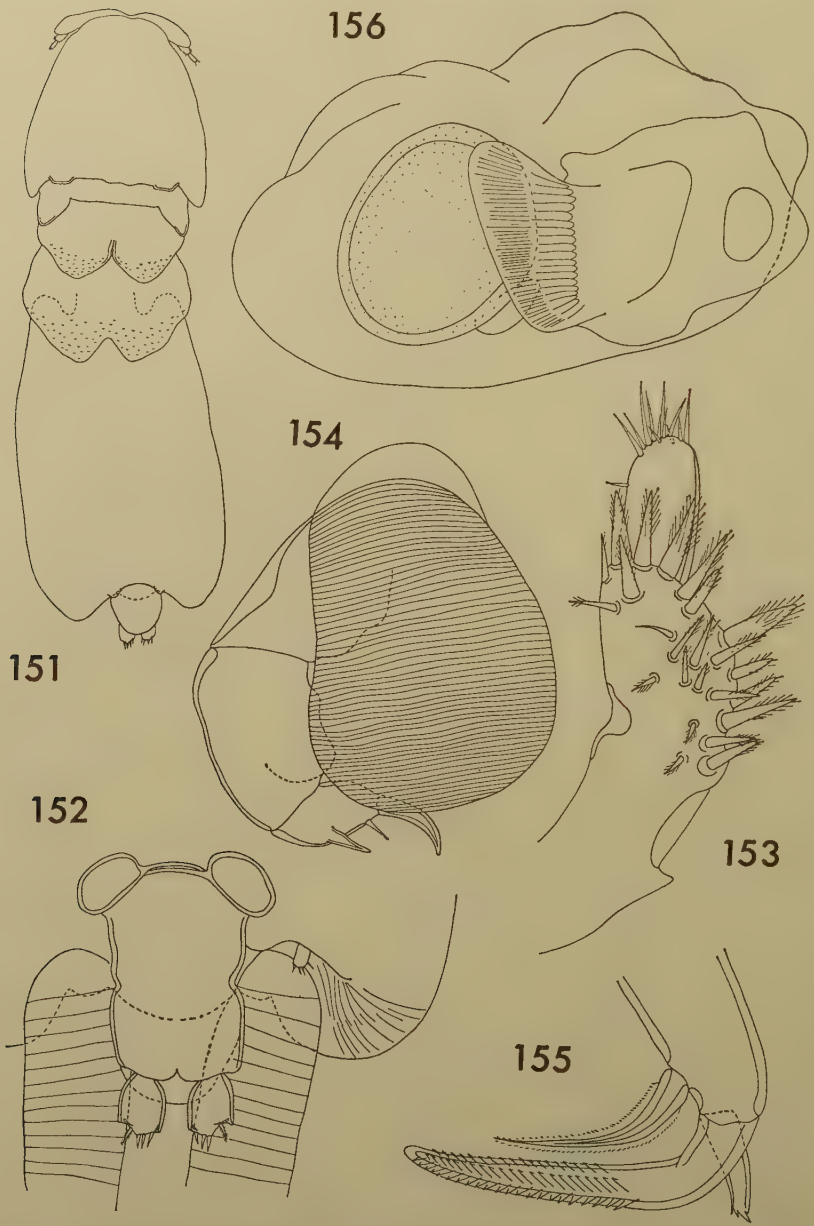
FIGURES 131–137.—*Phyllothereus cornutus*, female: 131, leg 1 (F); 132, leg 2 (C); 133, leg 3 (C); 134, leg 4 (C); 135, area of leg 5 (F). Male: 136, dorsal (A); 137, leg 5 (G).



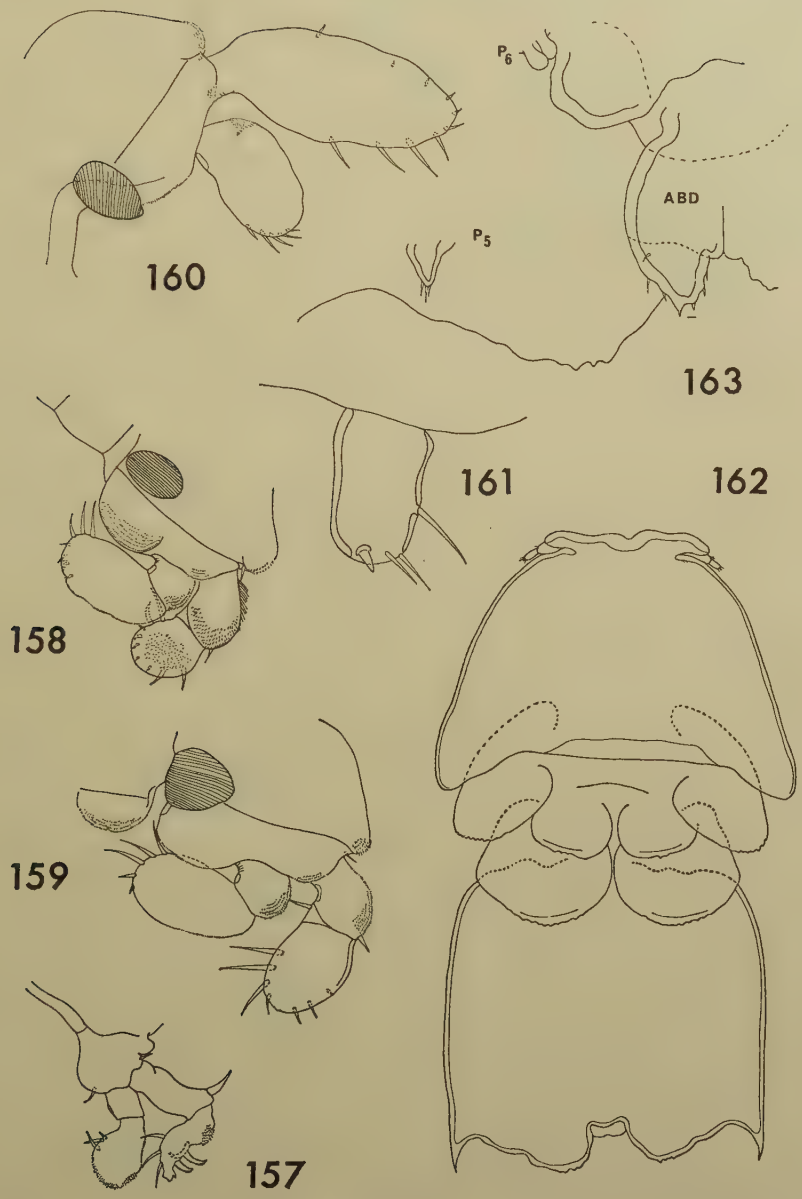
FIGURES 138–143.—*Phyllothereus cornutus*, male: 138, area of leg 6 (G). *Gangliopus pyriformis*, female: 139, dorsal (A); 140, mouth tube with adjoining adhesion pad (D); 141, leg 5 (G); male: 142, dorsal (B); 143, genital segment and abdomen, ventral (C).



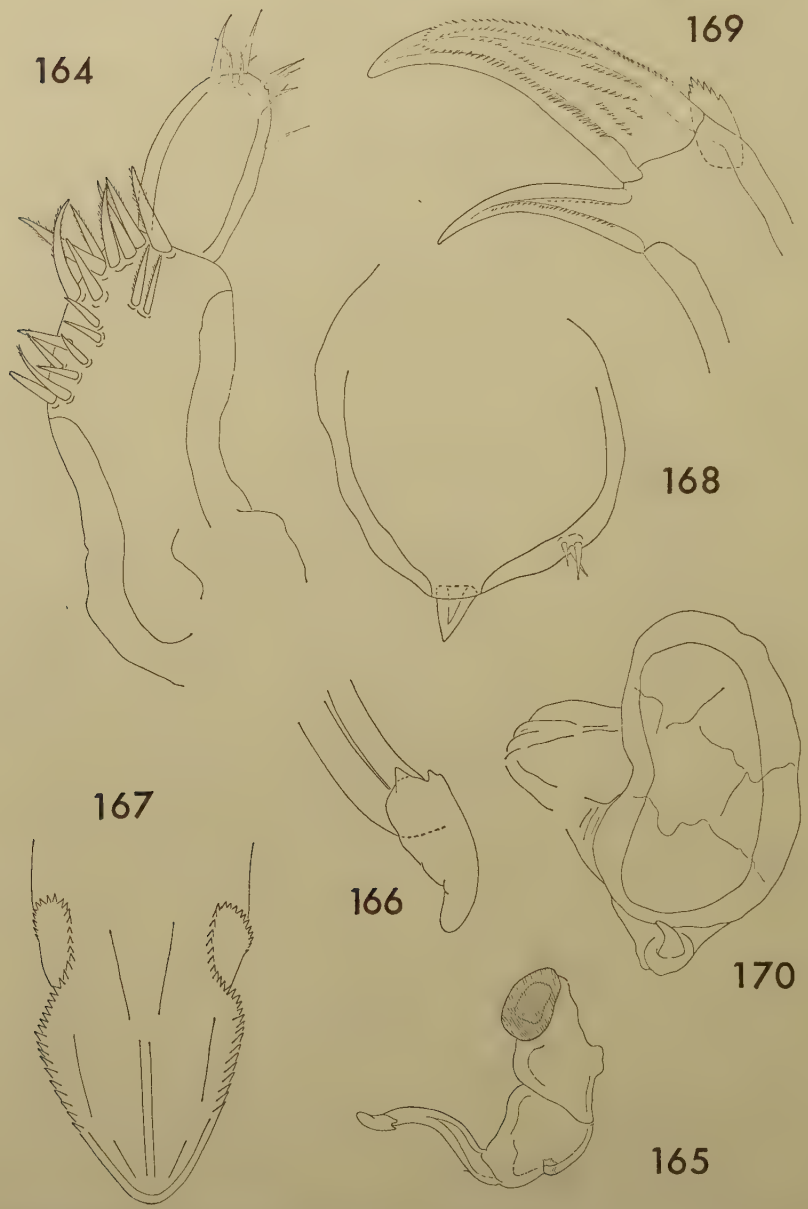
FIGURES 144–150.—*Gangliopus pyriformis*, male: 144, maxilliped (D); 145, leg 5 (E); 146, leg 6 (E). *Pseudopandarus gracilis*, female: 147, dorsal (C); 148, abdomen and caudal rami, ventral (G); 149, tip of second maxilla (H); 150, maxilliped (F).



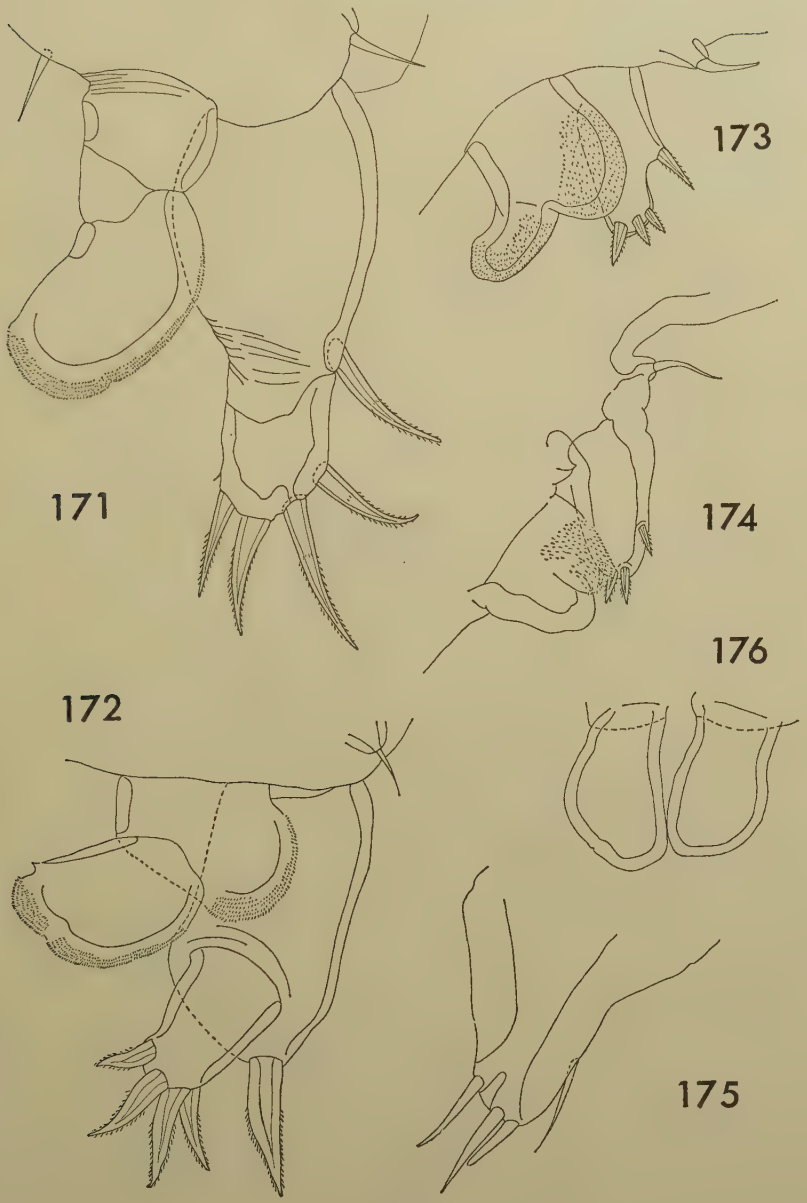
FIGURES 151–156.—*Pseudopandarus longus*, female: 151, dorsal (C); 152, abdomen and caudal rami, ventral (C); 153, first antenna (E); 154, second antenna (E); 155, tip of second maxilla (H); 156, maxilliped (D).



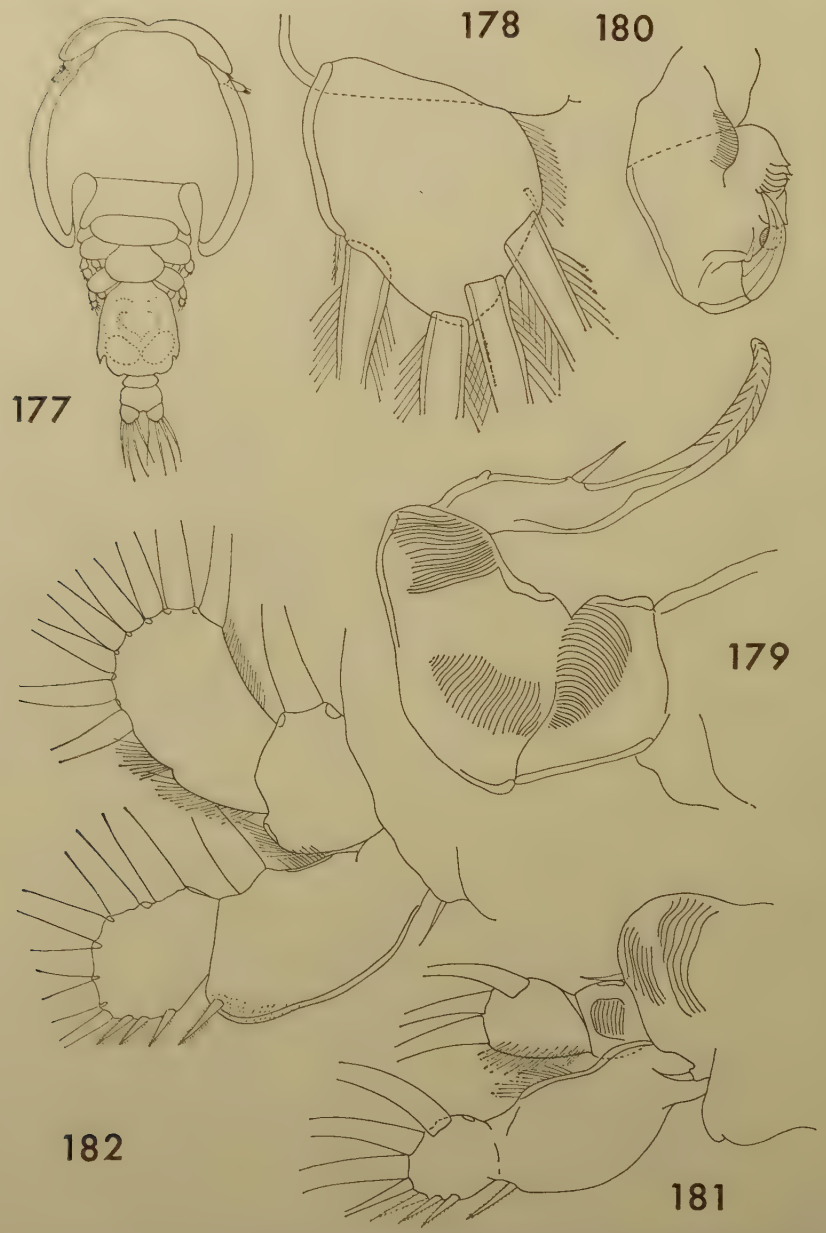
FIGURES 157–163.—*Pseudopandarus longus*, female: 157, leg 1 (G); 158, leg 2 (G); 159, leg 3 (G); 160, leg 4 (G); 161, leg 5 (H). *Perissopus dentatus*, female: 162, dorsal (C); 163, abdomen and adjacent area, ventral (D).



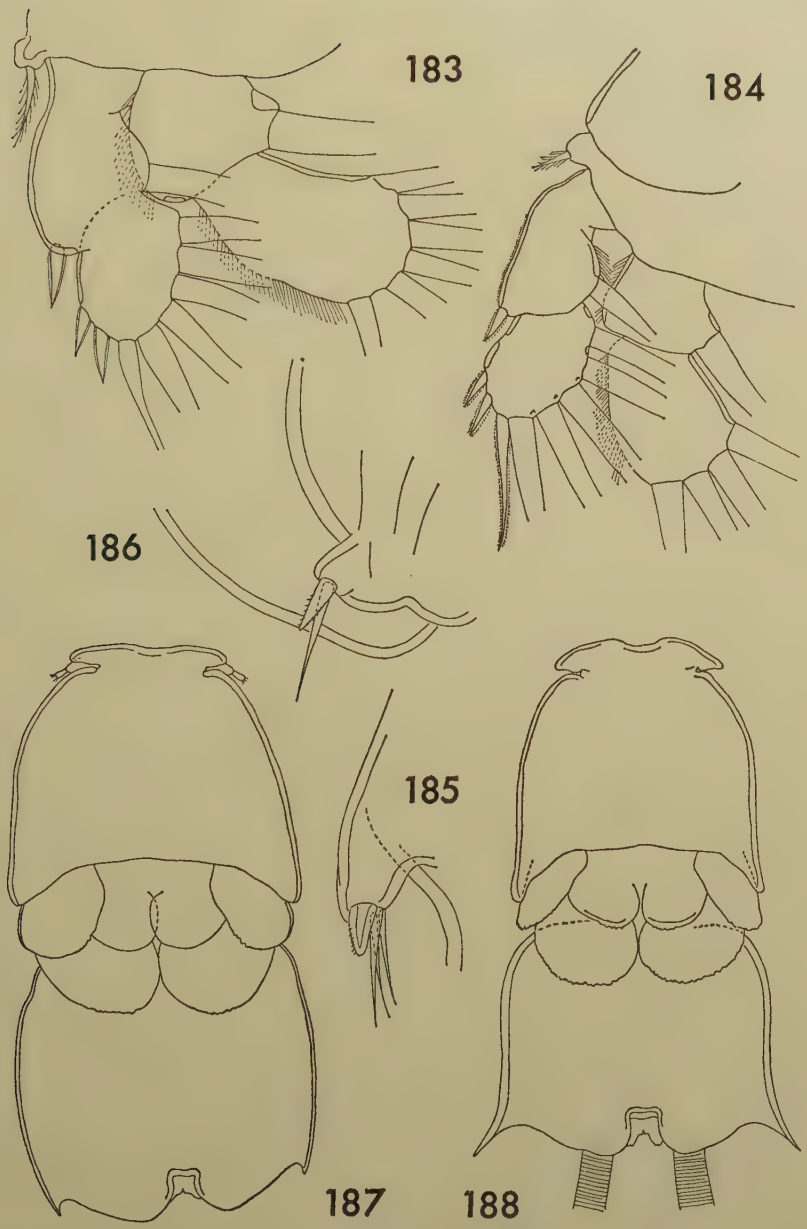
FIGURES 164–170.—*Perissopus dentatus*, female: 164, first antenna (E); 165, second antenna (G); 166, tip of second antenna (H); 167, tip of labium (I); 168, first maxilla (E); 169, tip of second maxilla (H); 170, maxilliped (D).



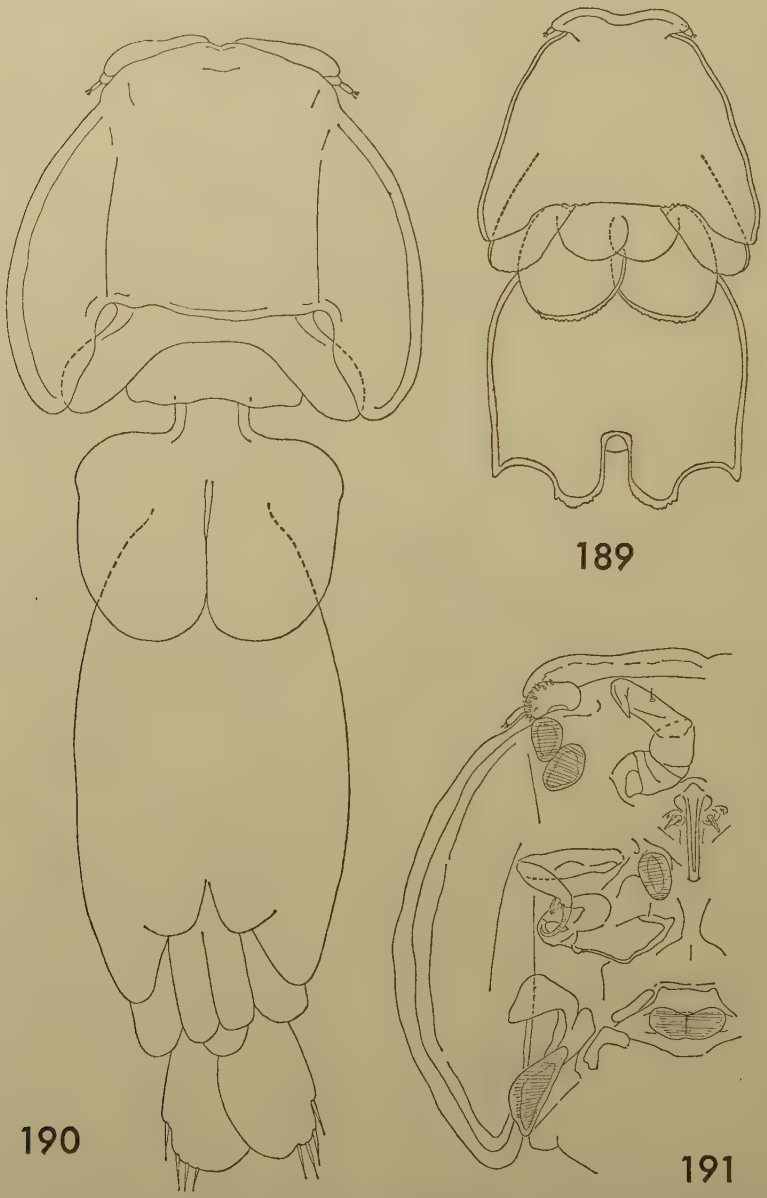
FIGURES 171–176.—*Perissopus dentatus*, female: 171, leg 1 (E); 172, leg 2 (E); 173, leg 3 (E); 174, leg 4 (E); 175, leg 5 (H); 176, leg 6 (H).



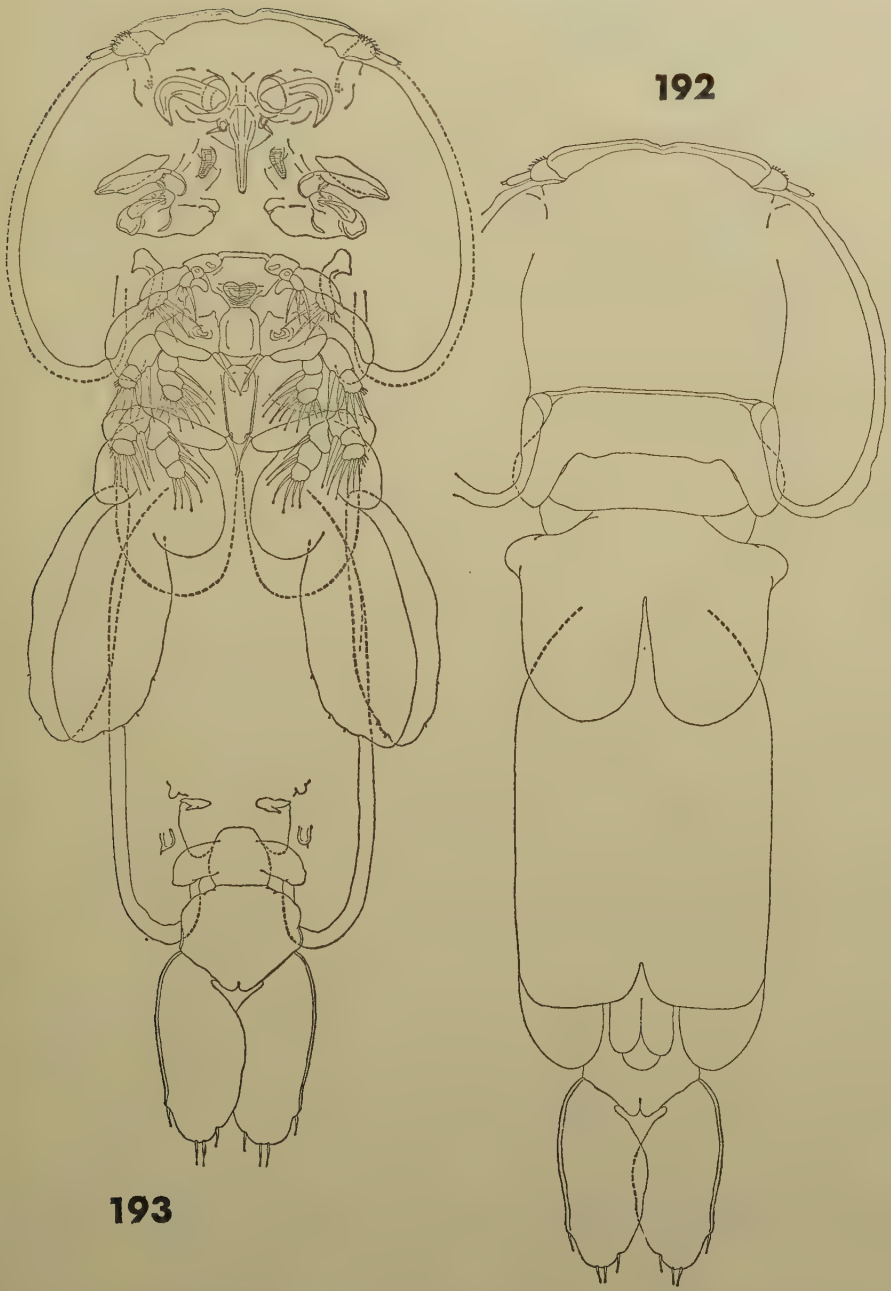
FIGURES 177–182.—*Perissopus dentatus*, male: 177, dorsal (F); 178, caudal ramus (E); 179, second antenna (E); 180, maxilliped (G); 181, leg 1 (E); 182, leg 2 (E).



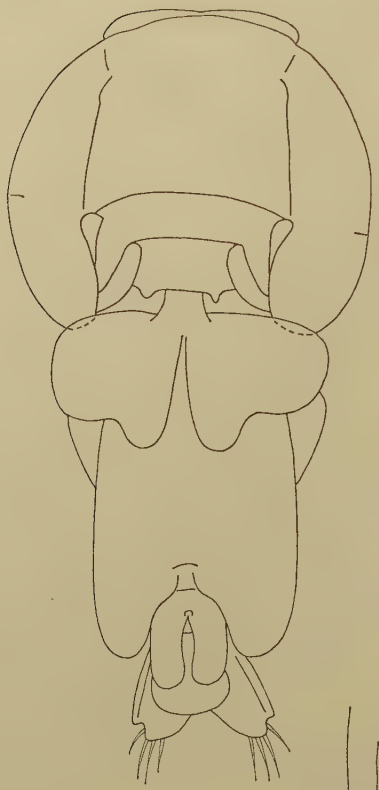
FIGURES 183–188.—*Perissopus dentatus*, male, 183, leg 3 (E); 184, leg 4 (E); 185, leg 5 (H); 186, leg 6 (H). Female: 187, dorsal (C); 188, dorsal (C).



FIGURES 189–191.—*Perissopus dentatus*, female: 189, dorsal (C). *Dinemoura producta*, female: 190, dorsal (A); 191, oral area (B).



FIGURES 192–193.—*Dinemoura ferox*, female: 192, dorsal (J); 193, ventral (J).



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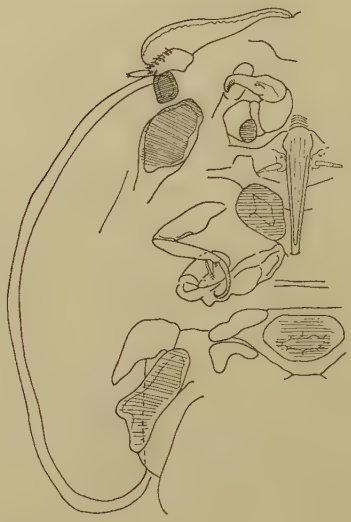

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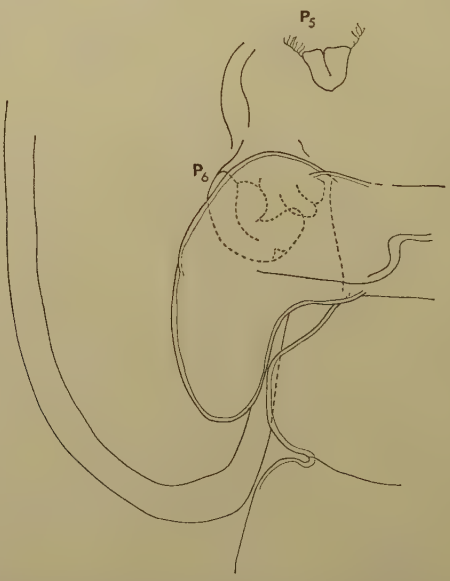
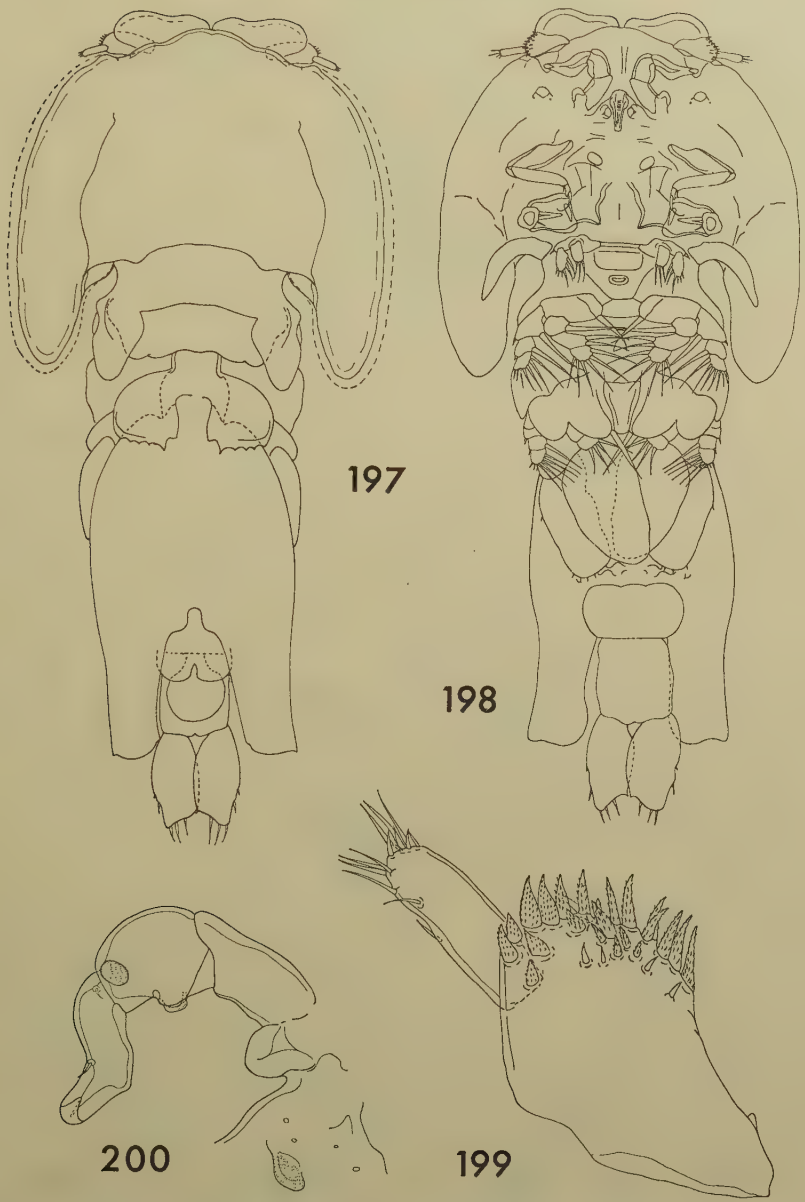


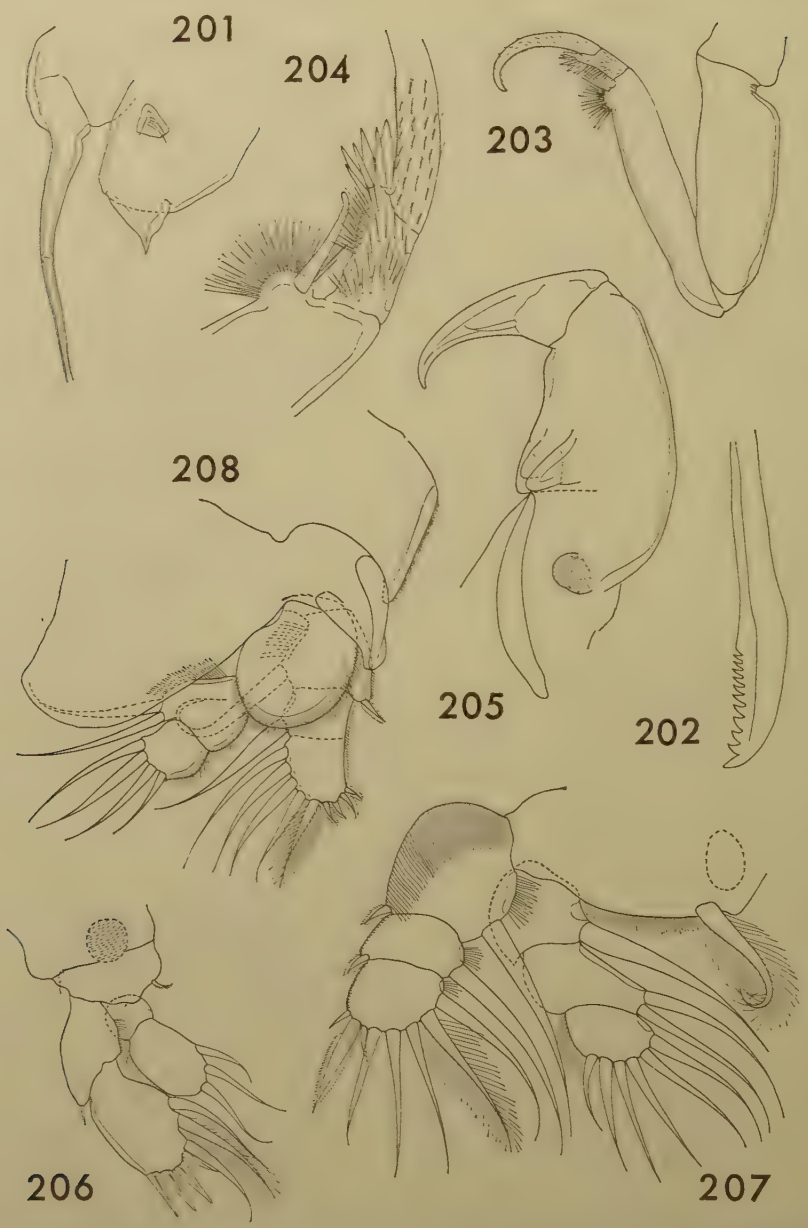
196

SCALE 1 0.05mm

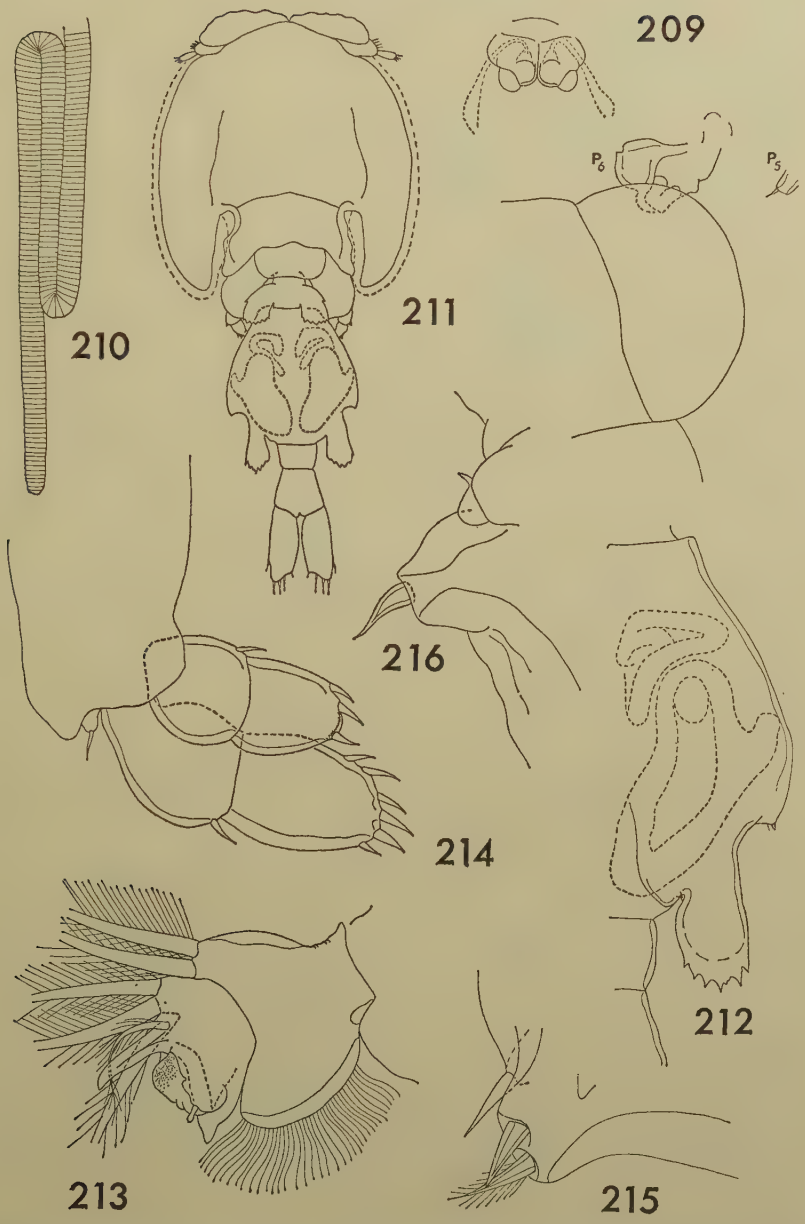
FIGURES 194–196.—*Dinemoura latifolia*, female: 194, dorsal (A); 195, oral area (B); 196, area of legs 5 and 6 (F).



FIGURES 197–200.—*Dinemoura discrepans*, new species, female: 197, dorsal (A); 198, ventral (A); 199, first antenna (D); 200, second antenna (F).



FIGURES 201–208.—*Dinemoura discrepans*, new species, female: 201, mandible and first maxilla (G); 202, tip of mandible (H); 203, second maxilla (F); 204, detail of claw of second maxilla (G); 205, maxilliped (F); 206, leg 1 (F); 207, leg 2 (F); 208, leg 3 (F).



FIGURES 209–216.—*Dinemoura discrepans*, new species, female: 209, area of legs 5 and 6 (F); 210, egg string (no scale) (10X). Male: 211, dorsal (A); 212, genital segment, ventral (C); 213, endopod of leg 3 (G); 214, leg 4 (G); 215, leg 5 (H); 216, leg 6 (E).

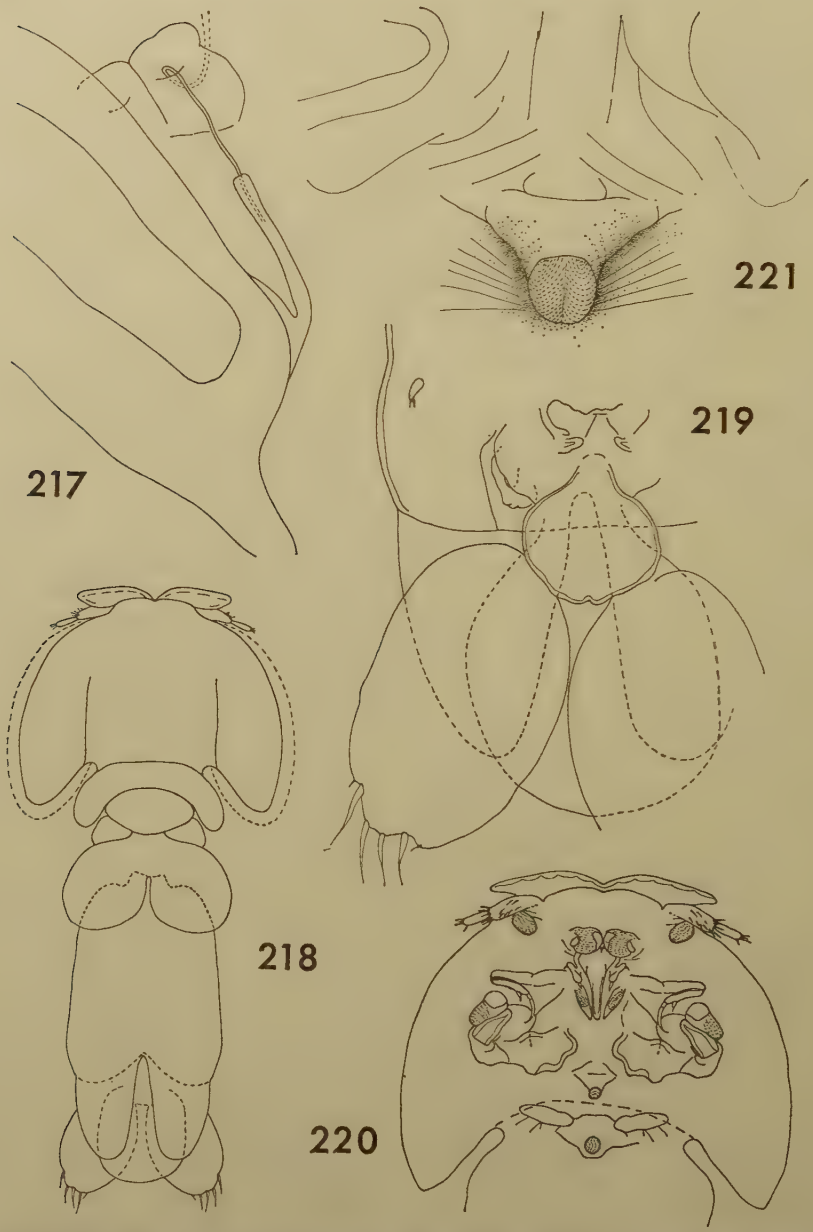
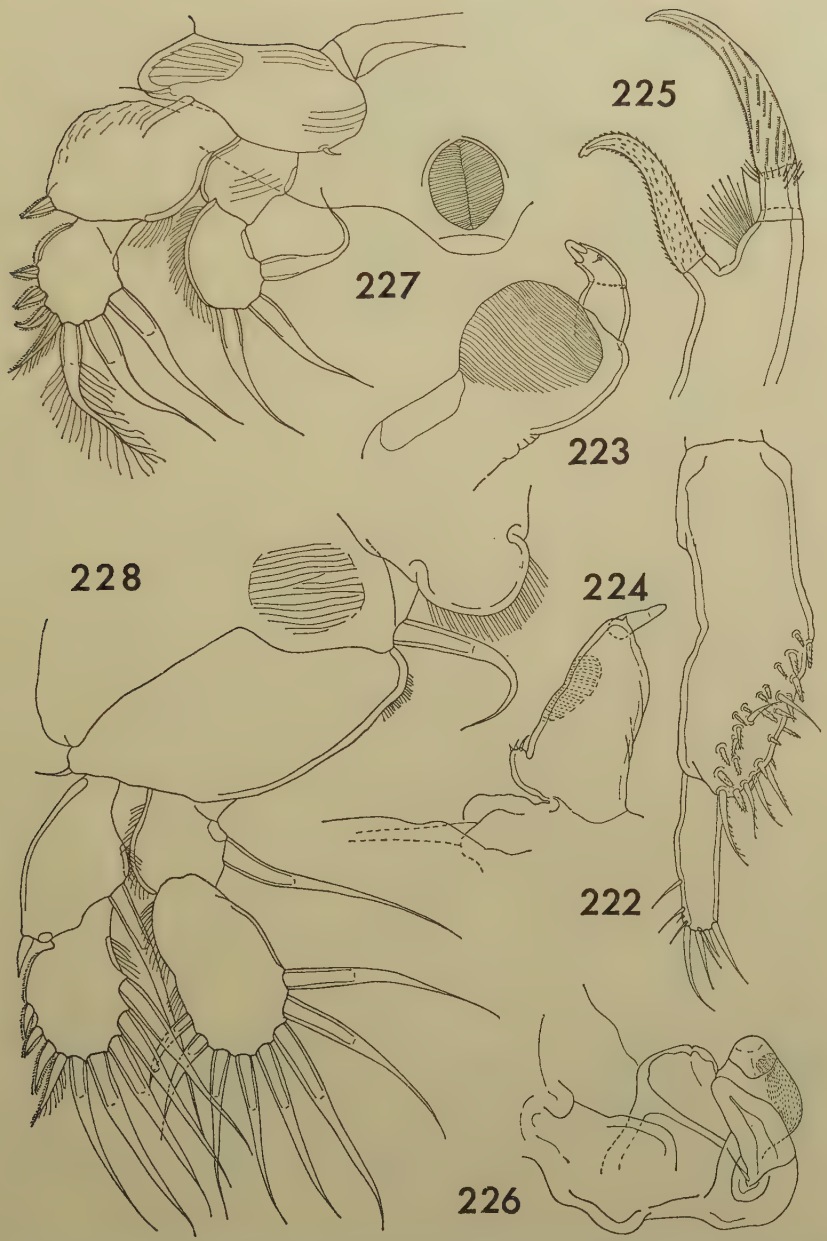
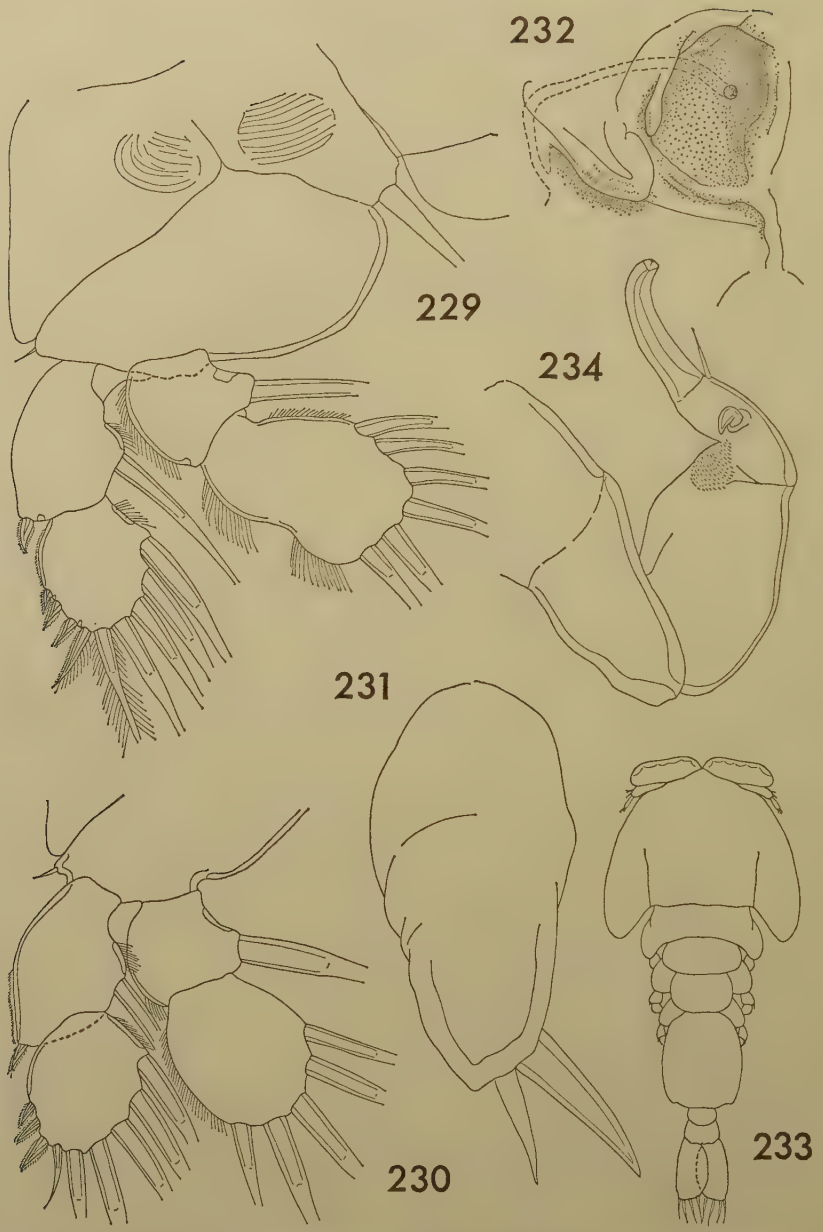


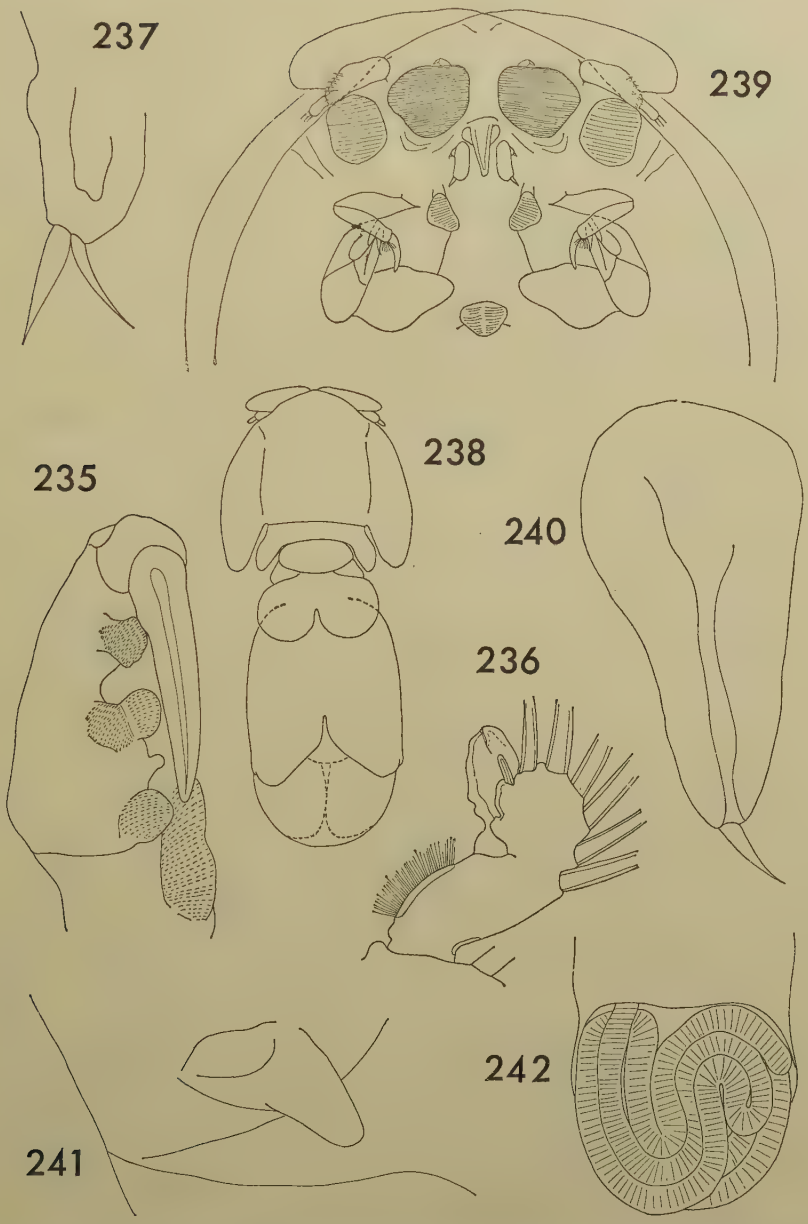
FIGURE 217–221.—*Dinemoura discrepans*, new species, male: 217, attachment area of spermatophore (E). *Demoleus heptatus*, female: 218, dorsal (A); 219, abdomen and caudal rami (C); 220, oral area (A); 221, process between maxillipeds (D).



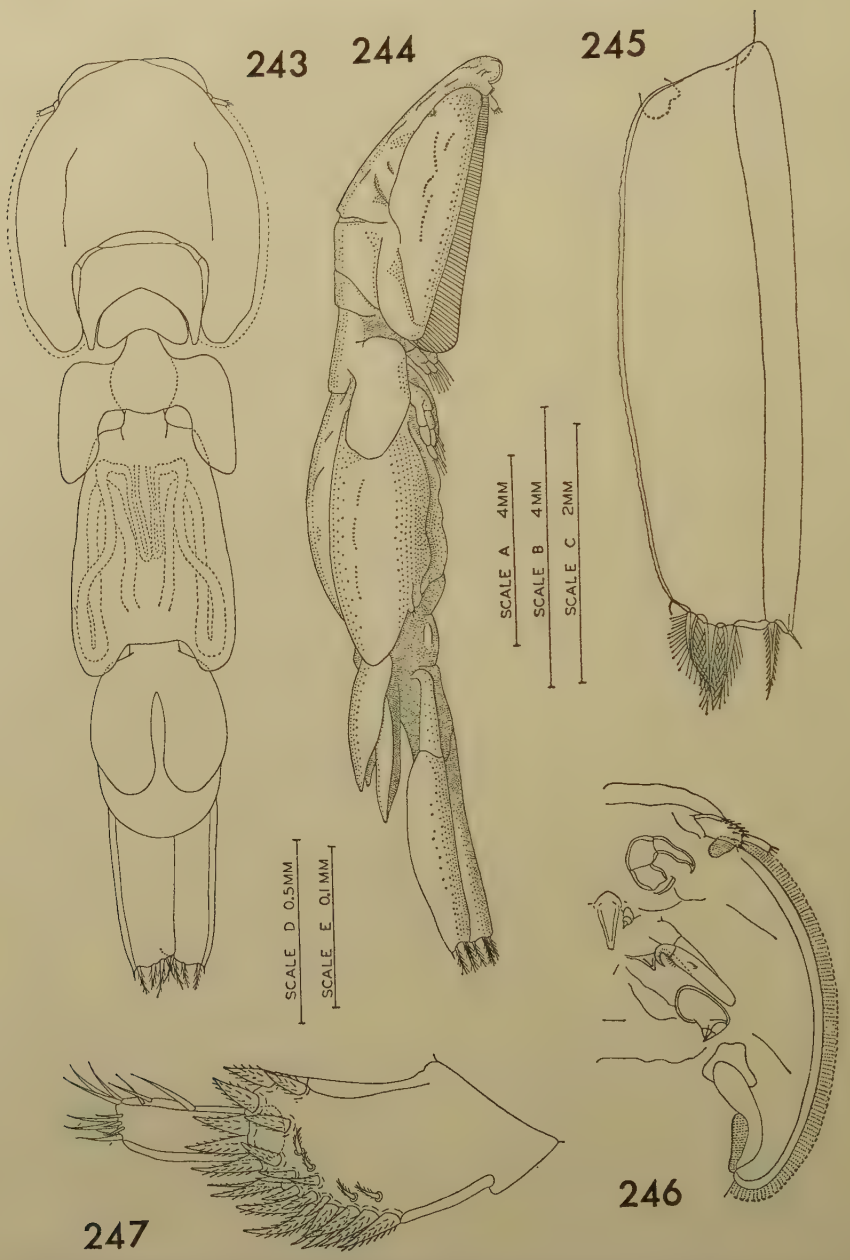
FIGURES 222–228.—*Demoleus heptatus*, female: 222, first antenna (D); 223, second antenna (D); 224, first maxilla (G); 225, claw of second maxilla (G); 226, maxilliped (F); 227, leg 1 (D); 228, leg 2 (D).



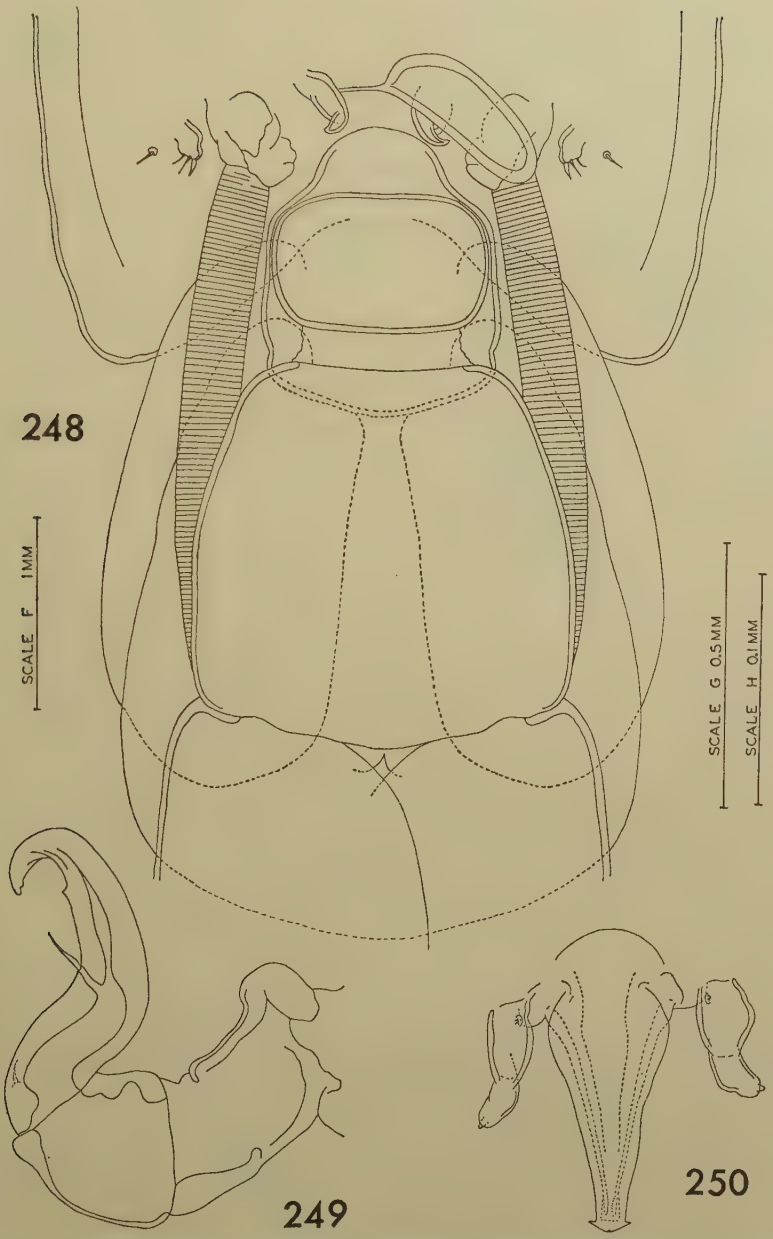
FIGURES 229–234.—*Demoleus heptatus*, female: 229, leg 3 (D); 230, leg 4 (D); 231, leg 5 (G); 232, leg 6 (G).



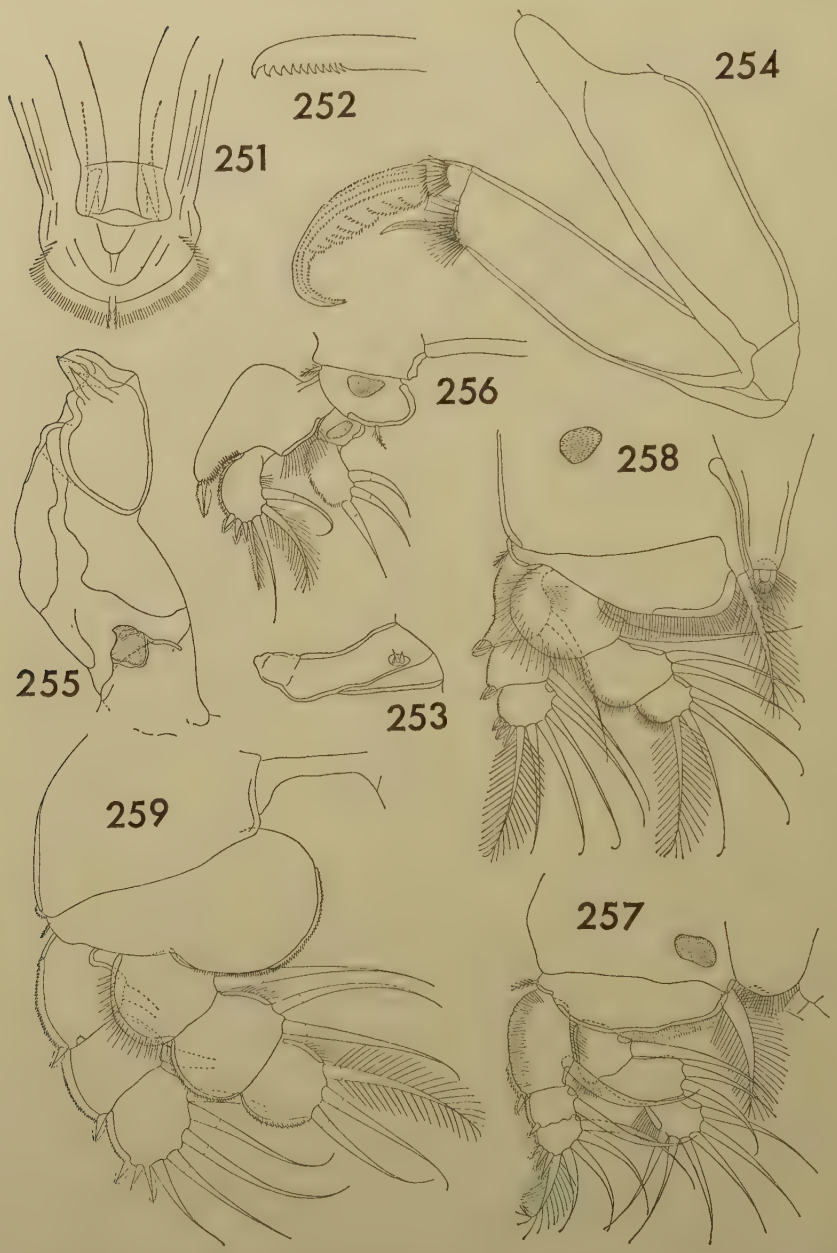
FIGURES 235–242.—*Demoleus hepta us*, male: 235, maxilliped (D); 236, endopod of leg 3 (D); 237, leg 6 (H). *D. latus*, female: 238, dorsal (A); 239, oral area (C); 240, leg 5 (E); 241, leg 6 (E); 242, egg strings, abdomen removed (B).



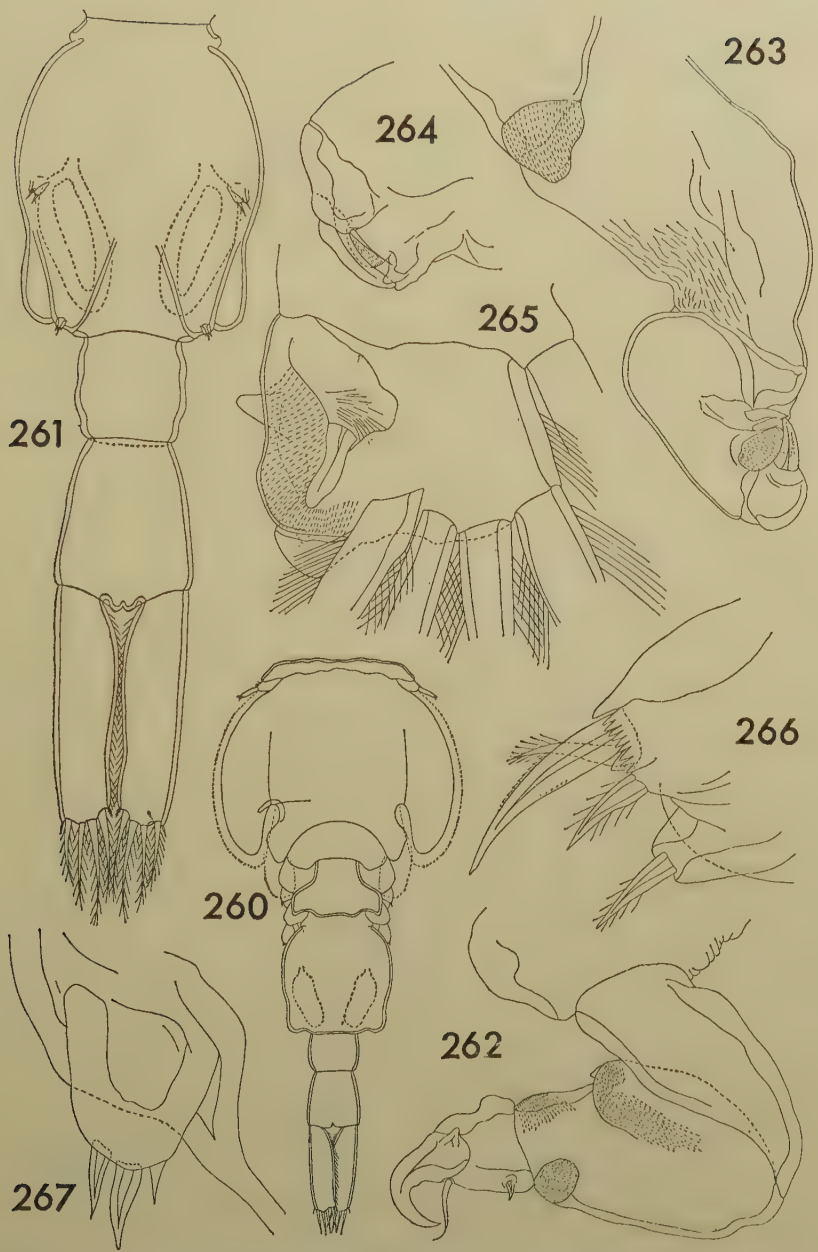
FIGURES 243–247.—*Pagina tunica*, female: 243, dorsal (A); 244, lateral (A); 245, caudal ramus (C); 246, oral area, ventral (D); 247, first antenna (E).



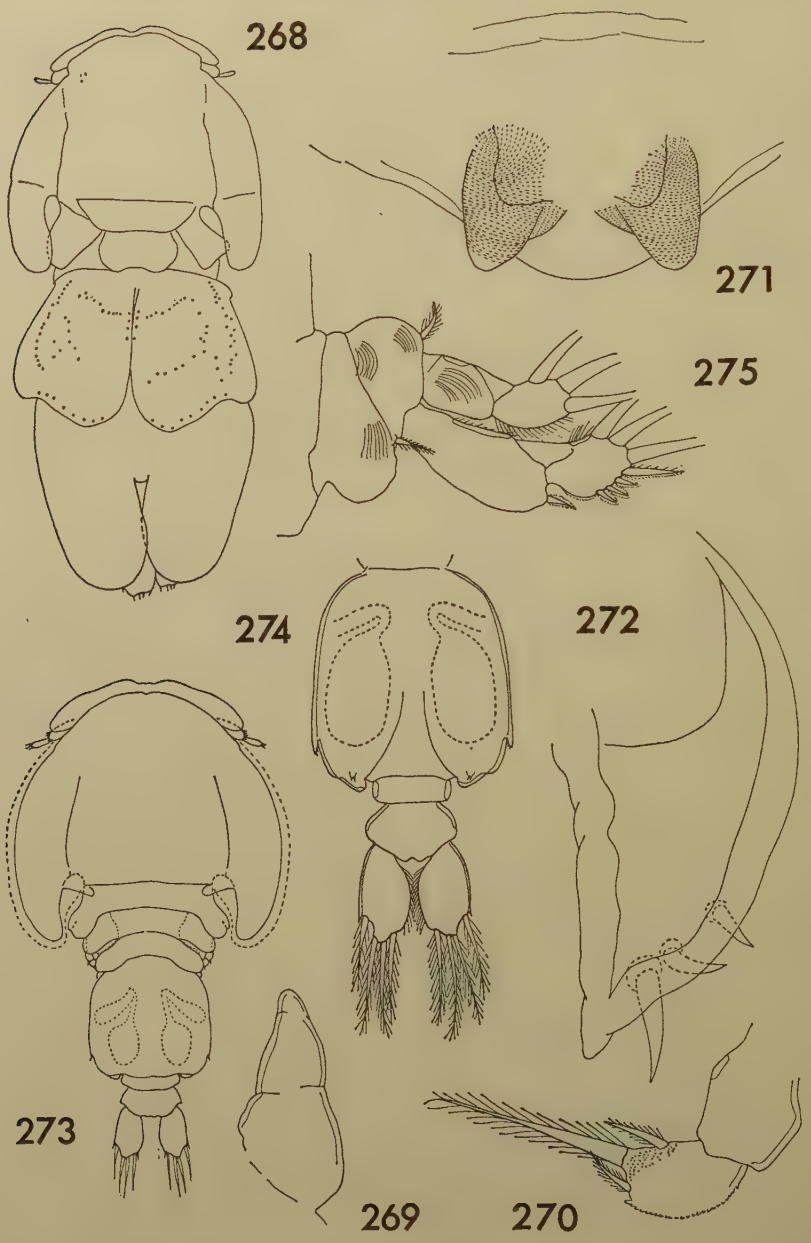
FIGURES 248–250.—*Pagina tunica*, female: 248, posterior end of genital segment and abdomen, ventral (B); 249, second antenna (E); 250, mouth tube and adjacent appendages, postero-lateral (E).



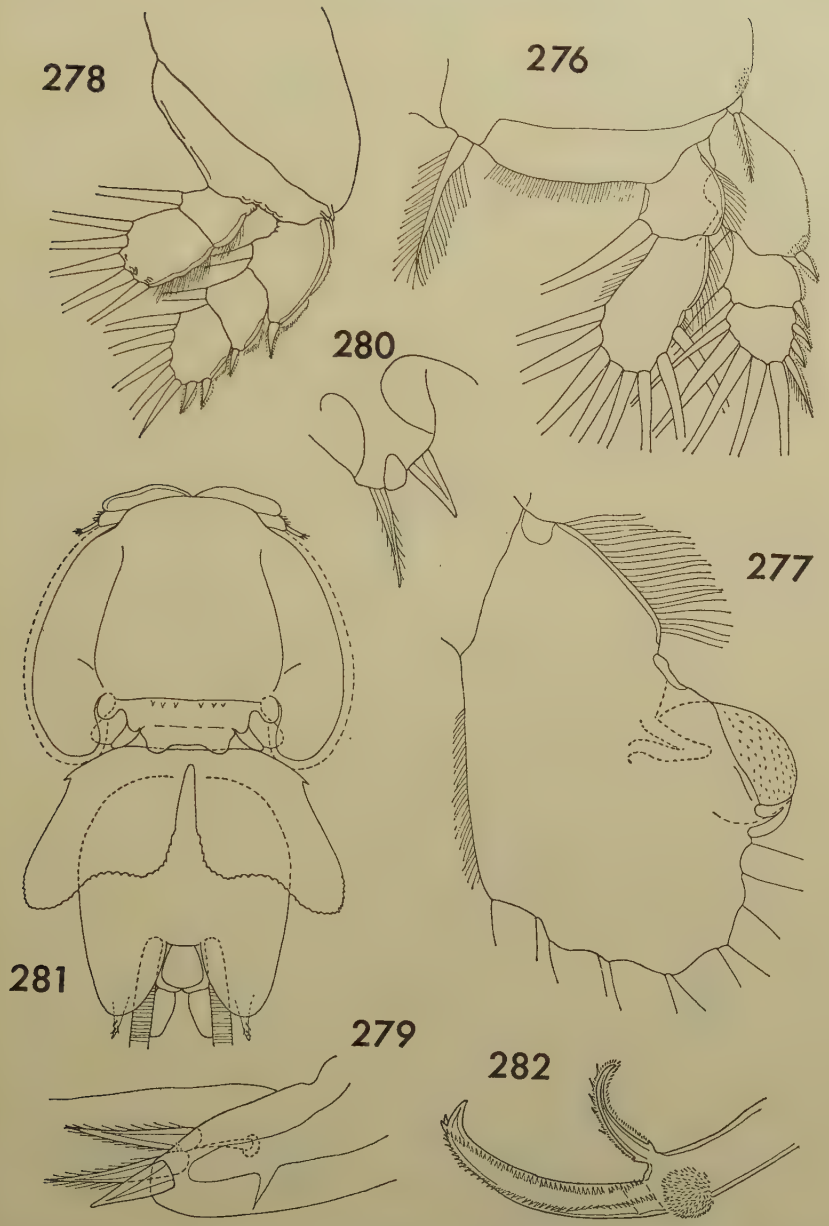
FIGURES 251–259.—*Pagina tunica*, female: 251, tip of mouth tube, antero-ventral (F); 252, tip of mandible (G); 253, first maxilla (H); 254, second maxilla (E); 255, maxilliped (B); 256, leg 1 (B); 257, leg 2 (B); 258, leg 3 (B); 259, leg 4 (B).



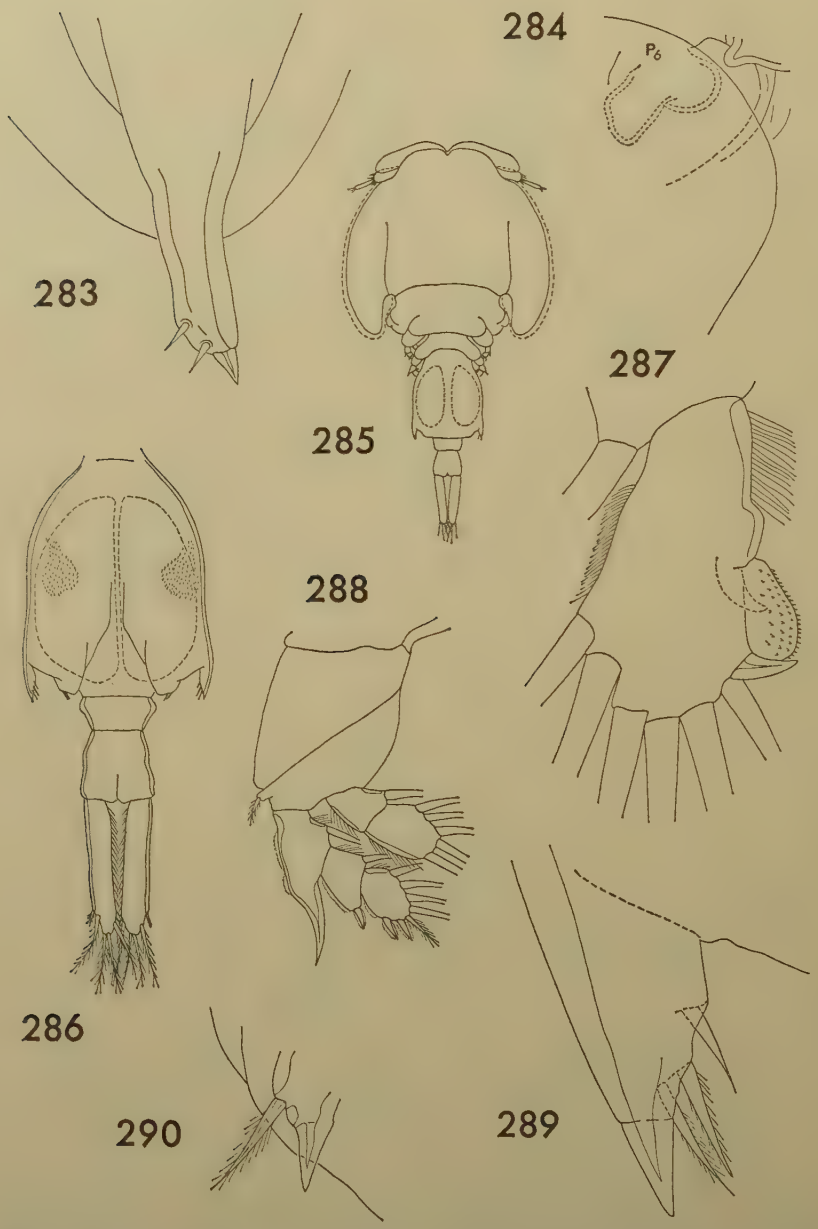
FIGURES 260–267.—*Pagina tunica*, male: 260, dorsal (A); 261, genital segment and abdomen, ventral (C); 262, second antenna (H); 263, maxilliped, ventral (E); 264, tip of maxilliped, dorsal (H); 265, leg 3, endopod, 3rd segment, ventral (F); 266, leg 5, left side (G); 267, leg 6 (G).



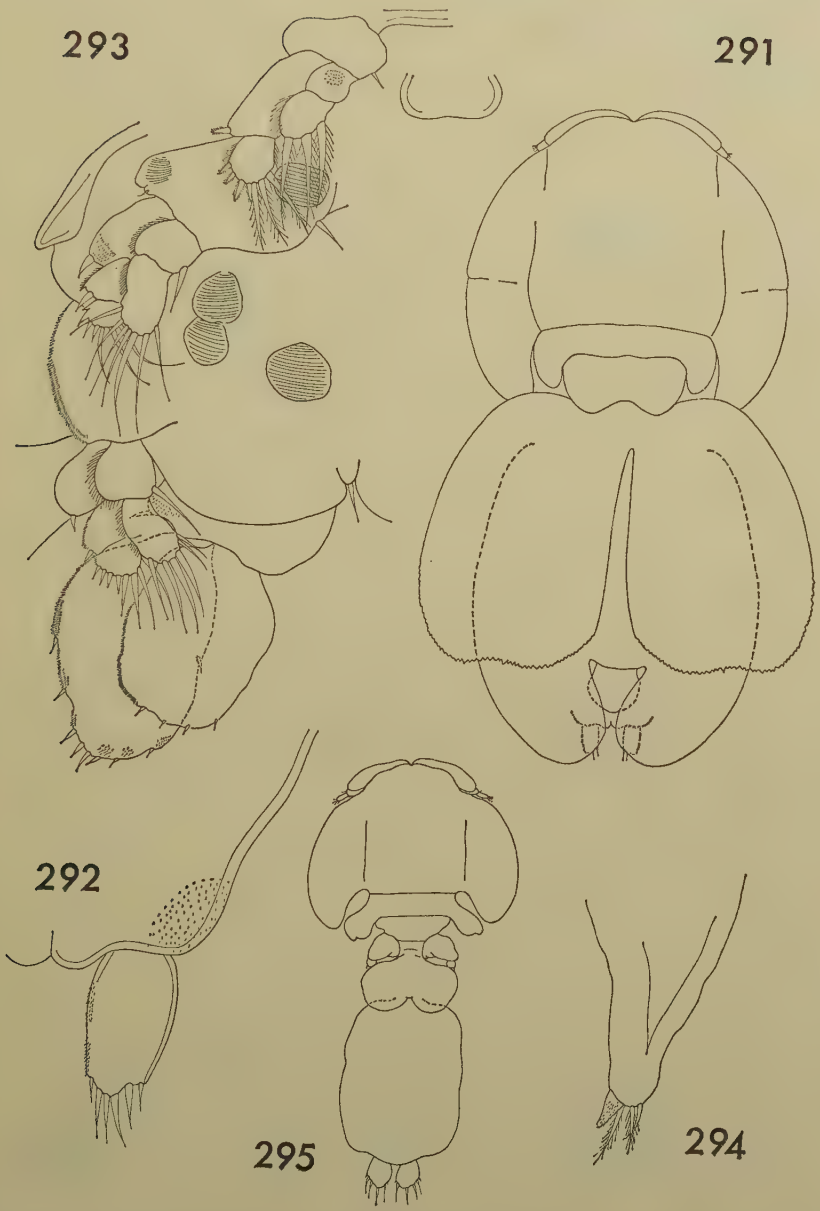
FIGURES 268–275.—*Echthrogaleus coleoptratus*, female: 268, dorsal (A); 269, first maxilla (G); 270, endopod of leg 1 (G); 271, process between legs 1 (G); 272, leg 5 (E). Male: 273, dorsal (B); 274, genital segment and abdomen (C); 275, leg 1 (G).



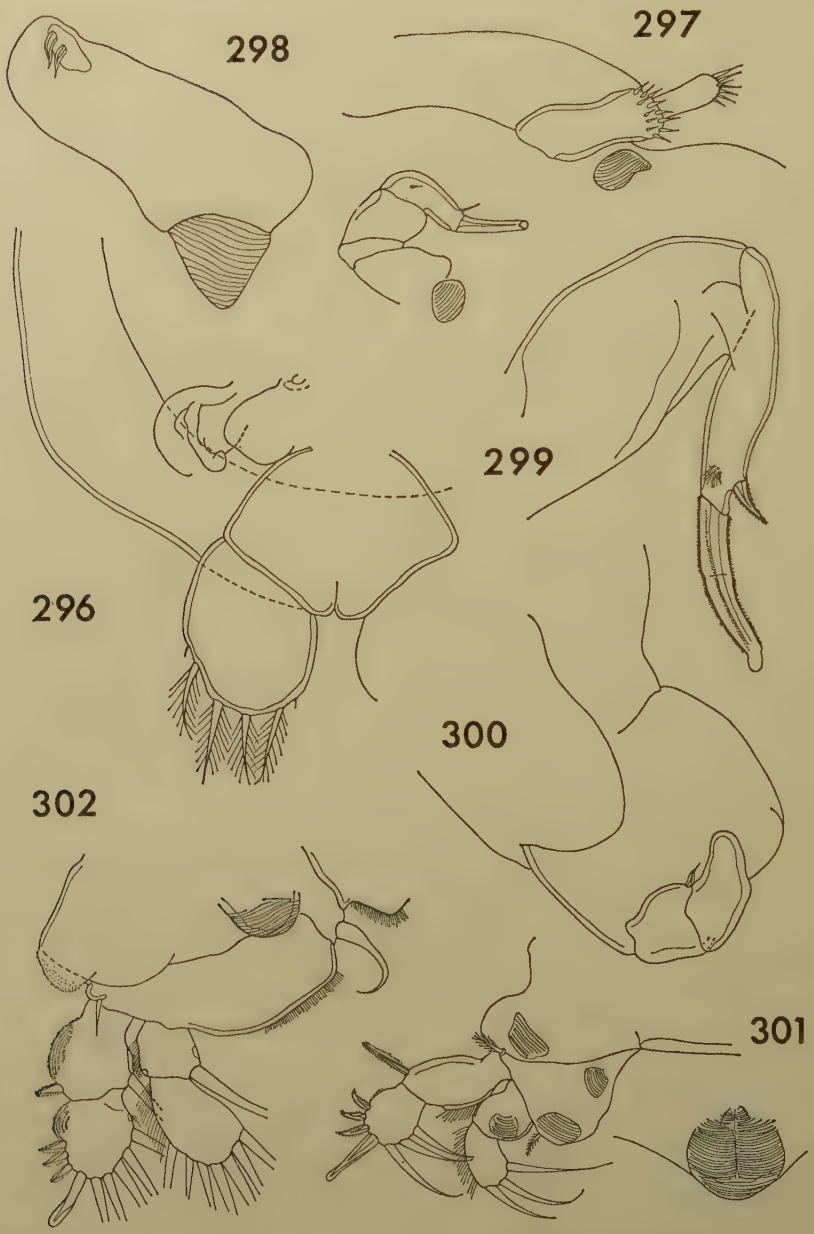
FIGURES 276–282.—*Echthrogaleus coleptratus*, male: 276, leg 2 (G); 277, endopod of leg 3 (E); 278, leg 4 (G); 279, leg 5 (H); 280, leg 6 (H). *E. denticulatus*, female: 281, dorsal (B); 282, second maxilla (G).



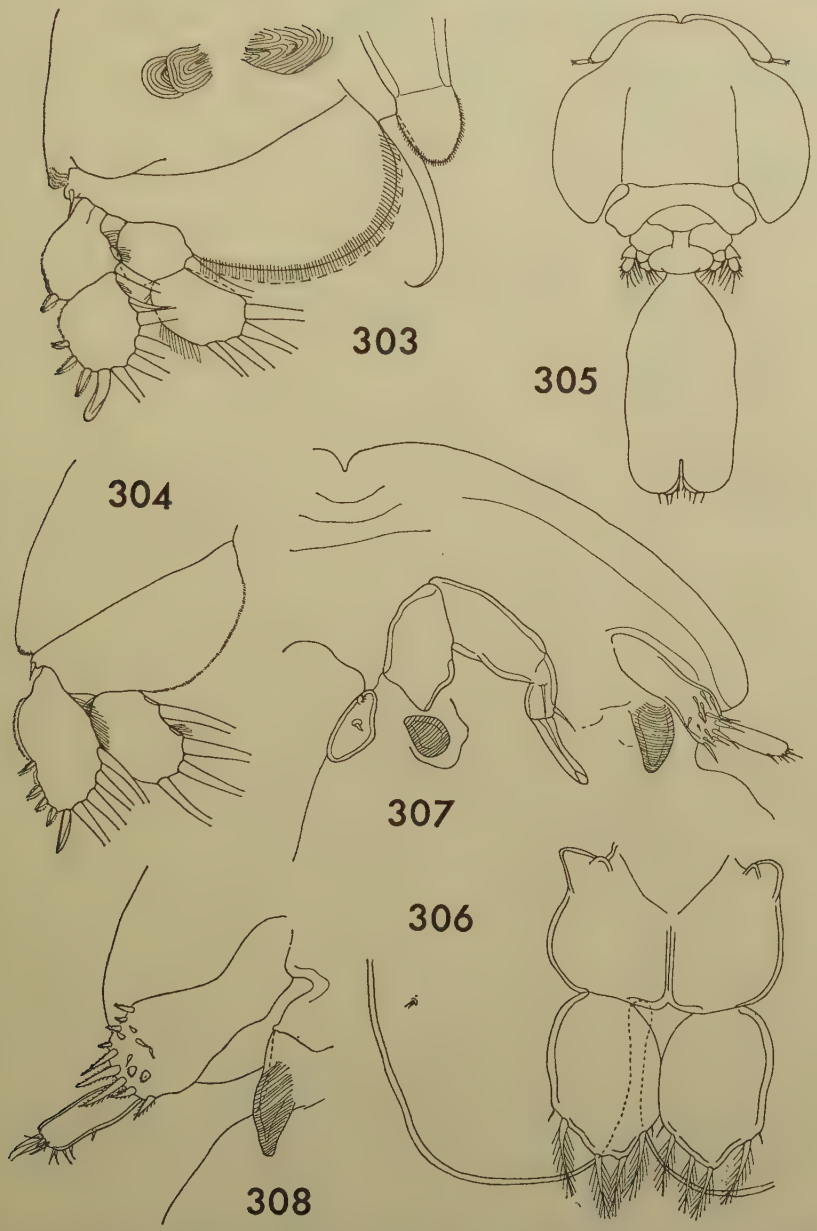
FIGURES 283–290.—*Echthrogaleus denticulatus*, female: 283, leg 5 (G); 284, leg 6 (G). Male: 285, dorsal (B); 286, genital segment and abdomen (F); 287, endopod of leg 3 (E); 288, leg 4 (G); 289, leg 5 (H); 290, leg 6 (H).



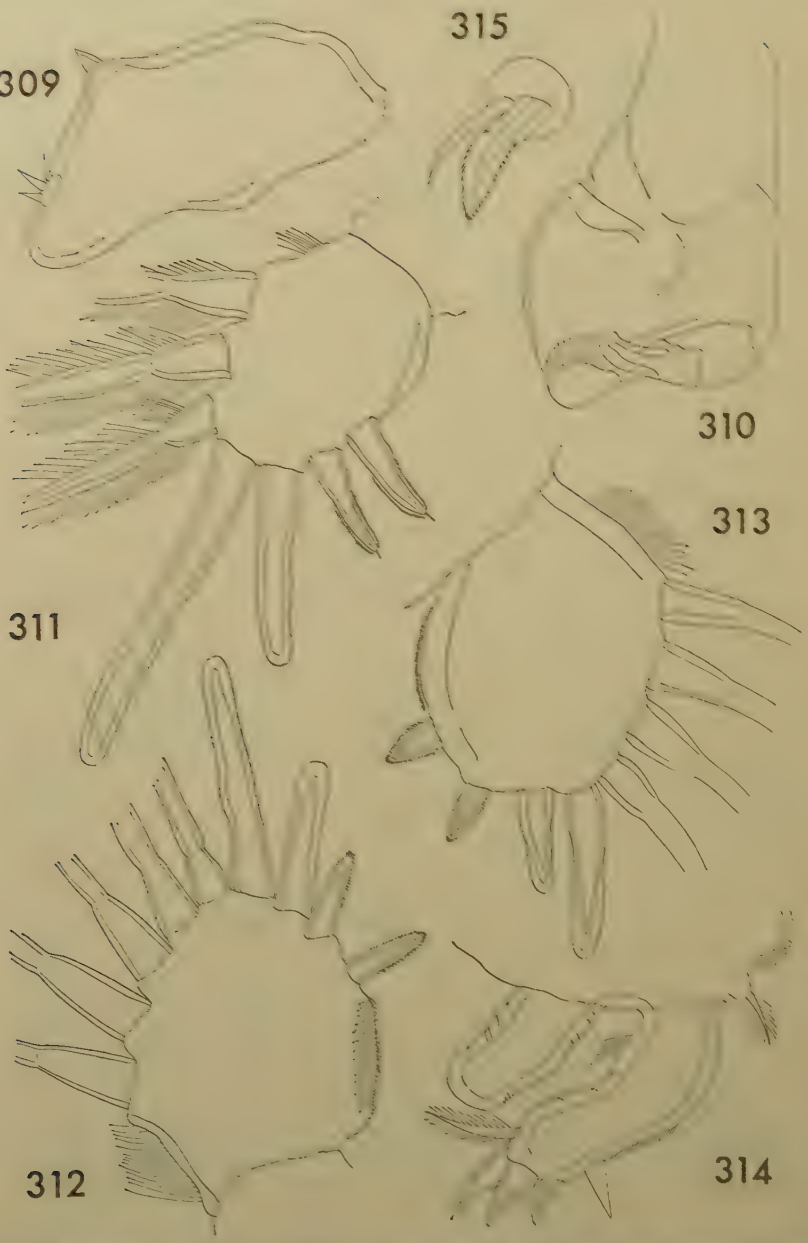
FIGURES 291–295.—*Echthrogaleus torpedinis*, female: 291, dorsal (A); 292, caudal ramus (F); 293, legs 1–4 (F); 294, leg 5 (G). *Nesippus orientalis*, female: 295, dorsal (B).



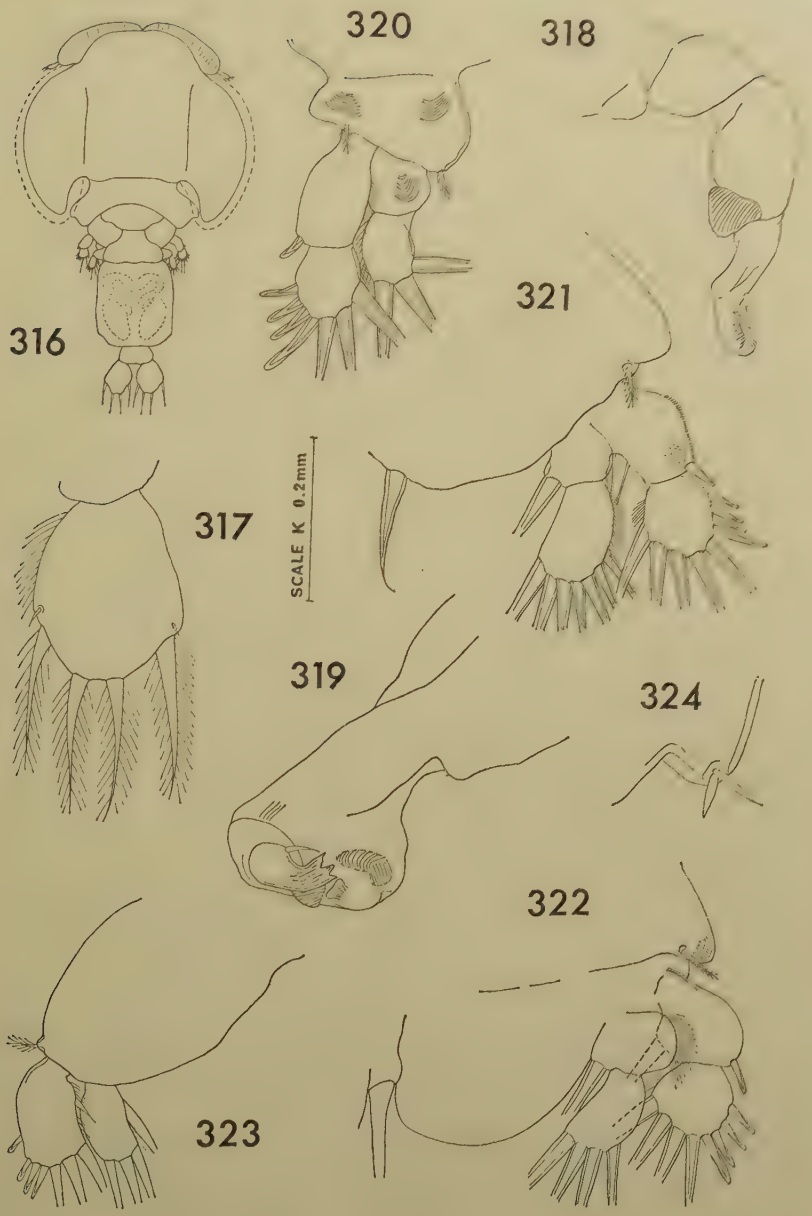
FIGURES 296–302.—*Nesippus orientalis*, female: 296, abdomen and caudal rami (D); 297, first and second antennae (D); 298, first maxilla (E); 299, second maxilla (G); 300, maxilliped (G); 301, leg 1 (G); 302, leg 2 (G).



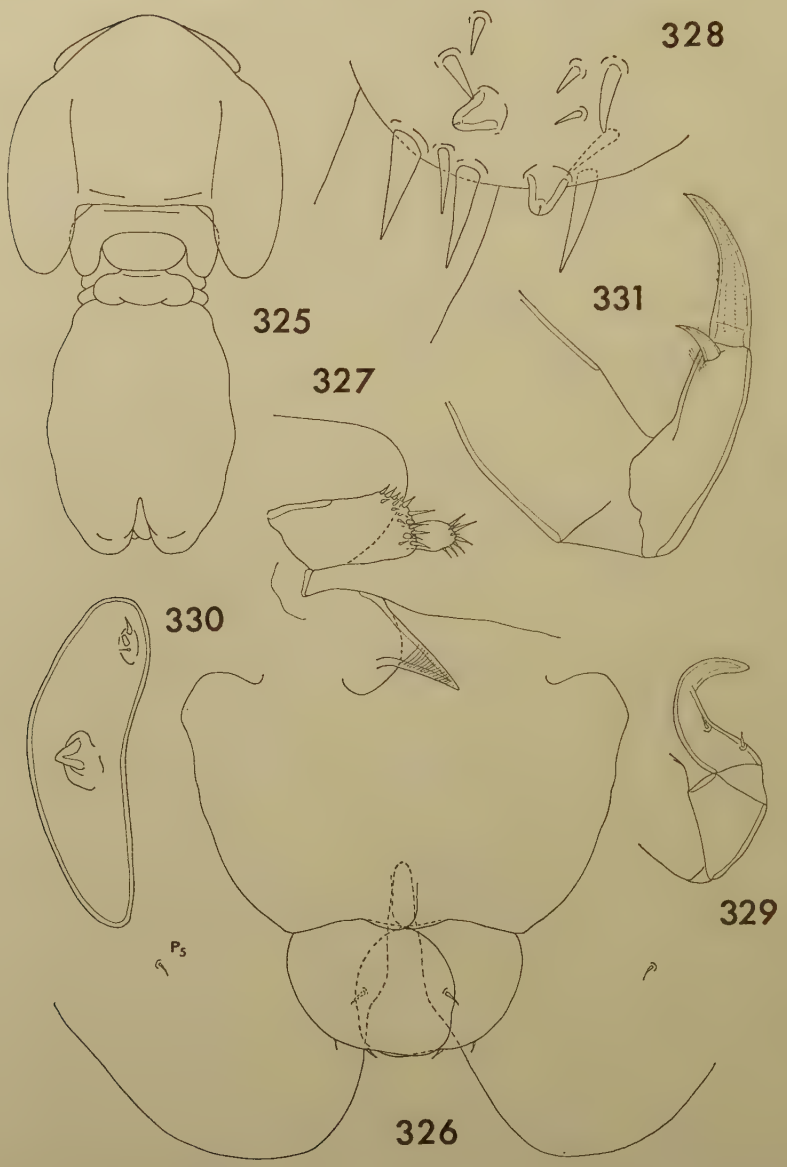
FIGURES 303–308.—*Nesippus orientalis*, female: 303, leg 3 (G); 304, leg 4 (G). *N. crypturus*, female: 305, dorsal (B); 306, abdomen and caudal rami (D); 307, first and second antennae (C); 308, first antenna (G).



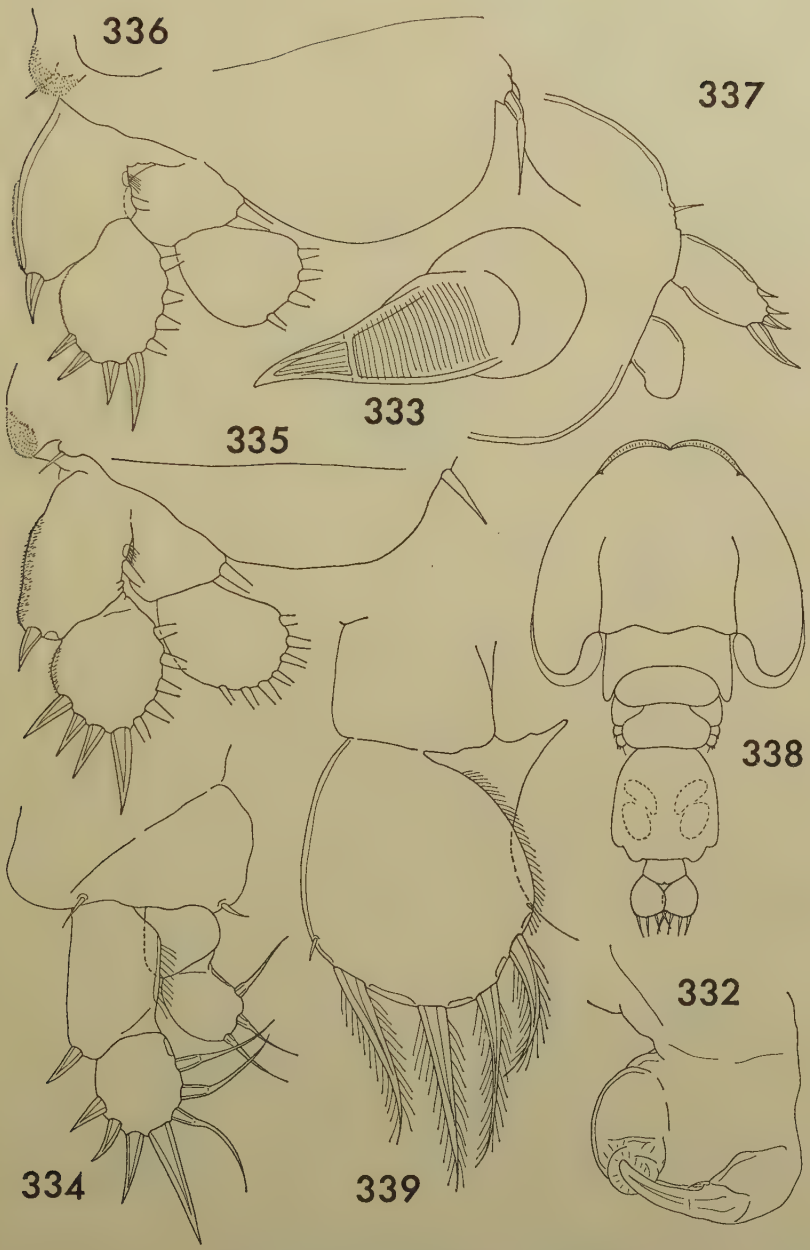
FIGURES 309–315.—*Nesippus crypturus*, female: 309, first maxilla (E); 310, maxilliped (G); 311, leg 1, last endopod segment (E); 212, leg 2, last endopod segment (E); 313, leg 3, last endopod segment (E); 314, leg 4 (E); 315, leg 5 (I).



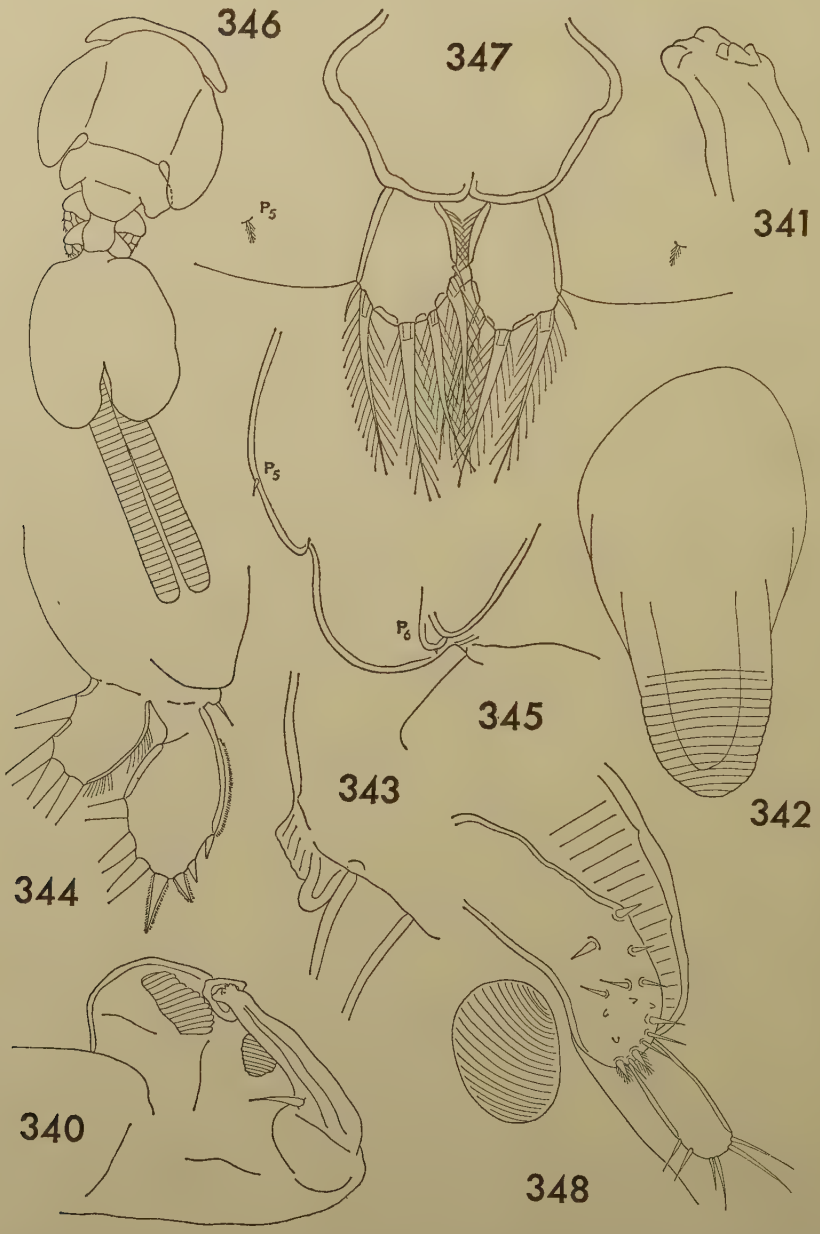
FIGURES 316–324.—*Nesippus crypturus*, male: 316, dorsal (B); 317, caudal ramus (G); 318, second antenna (G); 319, maxilliped (G); 320, leg 1 (K); 321, leg 2 (K); 322, leg 3 (K); 323, leg 4 (K); 324, leg 5 (H).



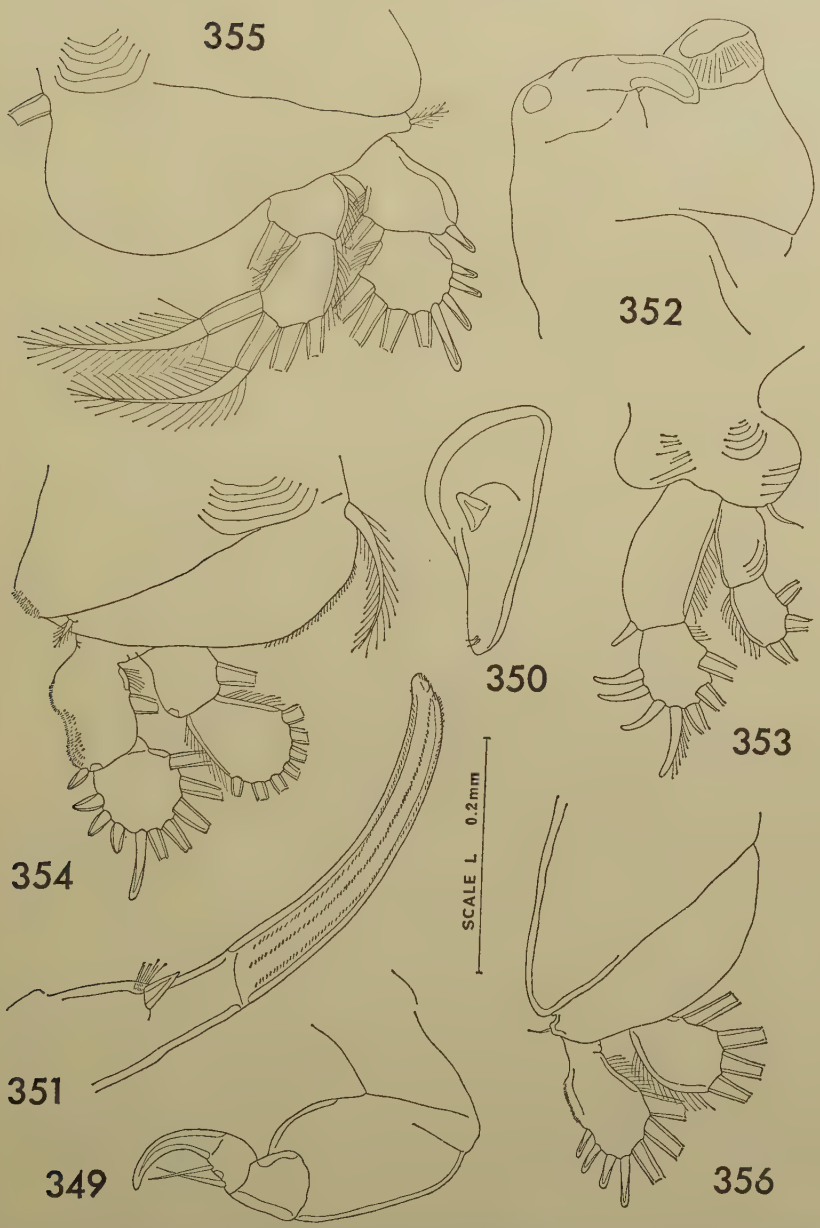
FIGURES 325–331.—*Nesippus tigris*, new species, female: 325, dorsal (B); 326, abdomen and caudal rami, ventral (D); 327, first antenna (D); 328, detail of first antenna (H); 329, second antenna (F); 330, first maxilla (L); 331, second maxilla (D).



FIGURES 332–339.—*Nesippus tigris*, new species, female: 332, maxilliped (D); 333, adhesions pad at base of maxilliped (K); 334, leg 1 (G); 335 leg 2 (G); 336, leg 3 (G); 337, leg 4 (G). Male: 338, dorsal (B); 339, caudal ramus (G).



FIGURES 340–348.—*Nesippus tigris*, new species, male: 340, maxilliped (G); 341, tip of maxilliped claw (H); 342, adhesion pad at base of maxilliped (E); 343, edge of last endopod segment of leg 3 (H); 344, leg 4 (G); 345, area of legs 5 and 6 (G). *N. vespa*, female: 346, dorsal (C); 347, abdomen and caudal rami (K); 348, first antenna (L).



FIGURES 349-356.—*Nesippus vespa*, female: 349, second antenna (L); 350, first maxilla (H); 351, claw of second maxilla (H); 352, maxilliped (L); 353, leg 1 (L); 354, leg 2 (L); 355, leg 3 (L); 356, leg 4 (L).

U.S. GOVERNMENT PRINTING OFFICE: 1967